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CO-EXISTENCE IN PHYTOPLANKTON: AN EXAMINATION OF HUTCHINSON'S SOLUTIONS TO THE "PARADOX OF THE PLANKTON"

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CO-EXISTENCE IN PHYTOPLANKTON: AN EXAMINATION OF HUTCHINSON'S SOLUTIONS TO THE "PARADOX OF THE PLANKTON"

by

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The “Paradox of the Plankton” was the response of Hutchinson (1961) to the apparent violation of the Principle of Competitive Exclusion in phytoplankton communities. One explanation for phytoplankton associations was that communities exist in a perpetual nonequilibrium and competition is never allowed to proceed to exclusion. However, current ecological theory argues that disturbance does not preclude the importance of niche differences among species, including those that involve competitive processes. I collected phytoplankton and limnological data over the winter mixing period in two monomictic reservoirs to determine if niche differences between species are relevant during mixing. I used ordination to assess the importance of environmental parameters to species abundance patterns, and then evaluated the significance of changes in abundance along ecological gradients versus neutral theory, which assumes niche differences are irrelevant to community assembly. Two flagellate species displayed different abundance patterns, where one was more abundant during deep mixing and high nutrient concentrations, while the other was favored under slight water column stability and relatively lower phosphorus concentrations. Also, the abundance of four large diatom species was distinct along axes that were described by light availability and mixing intensity. The abundance of all species was significantly outside of the predictions of neutral theory. These results emphasize that non-neutral

niche differences are relevant to community assembly and suggest that competitive processes cannot be ignored during disturbance.

Hutchinson also noted that the paradox may be "specious" and the lake environment is less homogenous than it appears. I used subsets of an extensive phytoplankton dataset to evaluate the effect of local sampling scale on the recognition of phytoplankton species abundance maxima and co-occurrence. Reduction of temporal or spatial scale resulted in considerable departures in the identification of abundance maxima for some species and created the illusion of coincident peaks in abundance between species. In addition, the use of presence/absence data and reduced sample scales created the appearance of co-occurrence between two species that in reality exhibited overlapping, but distinct, distributions. These results suggest caution in using phytoplankton associations as ecological indicators.

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CHAPTER 1. Hutchinson's Solutions to the Paradox of the Plankton: Spatial Heterogeneity and Nonequilibrium

The "Paradox of the Plankton" was the response of Hutchinson (1961, 1967) to his observation of the violation of Gause's principle of competitive exclusion (Hardin, 1960) in phytoplankton communities, and since has been a highly cited thesis and debated topic not only in phytoplankton community ecology, but in broader ecological theory. He observed that the principle of competitive exclusion does not hold for "phytoplankton associations", or groups of species that frequently co-occur, because the species compete for the same resources yet fail to reach a final competitive equilibrium.

Hutchinson (1967) suggested that the paradox could be addressed, albeit partially, if two species differ in requirements for trace nutrients versus major nutrients, in losses to predation, or in susceptibility to hydrological forces. This concept, described by Hardin as the "axiom of inequality" (1960), has since been supported as the necessary underpinning to coexistence (Chesson, 2000; Chase and Leibold, 2003). That is, coexisting species must have distinct ecological niches (Chesson, 1991), owing to traits that confer tradeoffs among the species. Resource competition theory (Tilman et al., 1982), for instance, demonstrated that two species are able to coexist in equilibrium if each is limited by a different resource. Under the theory, a species differs from other species in minimum requirements (R*) for potentially limiting resources in order to maintain net growth over losses, and a species experiences tradeoffs in its requirements for different resources. Coexistence under the theory occurs when each species has a greater impact on the resource that is most limiting to its net growth (intraspecific competition is greater than interspecific competition; Chesson, 2000; Chase and Leibold, 2003) and therefore diversity will equal the number of limiting resources. Indeed, Interlandi and Kilham (2001) and Grover and Chrzanowski (2004) demonstrated that resource competition is a valid explanation of phytoplankton community structure in lakes by relating diversity to the number of limiting resources.

Hutchinson (1967) noted that predation would result in coexistence of two species if the better competitor is more susceptible to a predator. Certainly, zooplankton display

different feeding habits and food preferences across phylogenetic groups and even within the life cycle of a single species. By changing the mortality rate of a population, predation increases the minimum resource level needed to sustain positive net growth. This can induce coexistence if the superior competitor also is preferentially consumed relative to the lesser competitor. In addition, predators can alter competitive processes of prey species by changing resource availability or by modifying resource use (reviewed in Chase et al., 2002). Other mechanisms of selective mortality, such as parasitism or differential susceptibility to physical factors, can similarly bring about coexistence if the superior competitor is differentially affected.

The most extensive explanation for the paradox given by Hutchinson (1961, 1967) was that phytoplankton communities exist in a perpetual nonequilibrium; therefore, competition is never allowed to proceed to exclusion, as seasonal change occurs on a time scale approximately equal to competitive exclusion. In other words, non-equilibrium conditions would nullify the assumption of equilibrium under the principle of competitive exclusion. Certainly, weather-related events, such as wind-induced mixing and rainfall are invoked as the primary nonequilibrium driver of high diversity in lakes (Padisák et al, 1993). Interlandi and Kilham (2001) and Grover and Chrzanowski (2004) found that exceptions to the diversity-limiting resource relationship were driven by disturbance. In the case of the latter, they found diversity to be significantly correlated to rainfall over the prior ten days in a small reservoir in north Texas. One explanation for increased diversity under variable environments was provided by Sommer (1984), who was able to induce coexistence of phytoplankton species in cultures when phosphorus was provided in pulses. He demonstrated that species classified as "storage specialists" coexisted with “velocity-adapted” species (those with higher phosphorus uptake and growth rates) when the mutual limiting nutrient was provided in pulses. Tradeoffs in minimum cell quota needed for net growth versus storage capacity can induce coexistence between species when nonequilibrium conditions include variability in phosphorus supply (Grover, 1991). Differences among species in nutrient uptake rates under fluctuating irradiance (such as during water column mixing) also can influence

competitive outcomes (Lichman et al., 2004). These findings are consistent with the argument that trait differences among species affect competition in the presence of disturbance (Chesson, 2000). Therefore, contrary to the presumption of Hutchinson (1967), competitive processes cannot be ignored during disturbance. Indeed, trade-offs can occur between tolerance to disturbance and competitive ability (Chase and Leibold, 2003).

Hutchinson (1967) also noted that the paradox might be "specious" in that the lake environment is less homogenous than it appears. While Hutchinson minimized the influence of the light gradient toward coexistence, others have found that flagellates differ in their preferences (Clegg et al., 2003) and even congenerics differ in growth rates (Gervais, 1997) across light gradients, contributing to vertical separation of species *in situ*. Algal growth rates and nutrient uptake rates (van Donk and Kilham, 1990) are a function of water temperature and the extent of the dependence varies across taxonomic groups, which may contribute to seasonal succession of phytoplankton. These and other factors that are spatially and temporally heterogenous within a lentic system can contribute to coexistence within a lake over years because of the diversity of niche opportunities over space and time within each growing season. Scale of observation therefore can have a profound effect on the recognition of species maxima and co-occurrence if it is coarser than the spatial or temporal pattern in community structure. Indeed, Interlandi et al. (1999) found that abundance maxima of species rarely co-occurred over space and time during the growing season across three lakes when they were viewed at a high spatial and temporal resolution. However, algal associations defined by Reynolds (1984) as "assemblages of species that share closely similar phasing of increase, relative abundance and decrease" are attributed to mutual adaptive traits (Reynolds et al., 2000), but may be an artifact of inappropriate sampling scale if the true species abundance maxima are separated by space and time.

The chapters that follow are an examination of the latter two arguments regarding Hutchinson's paradox. First, I further explore the effect of disturbance on phytoplankton community structure. While Hutchinson (1967) assumed that competitive exclusion

theory is irrelevant outside of equilibrium, disturbance does not necessarily preclude the influence of niche differences among species on community structure, including those that define competitive ability (Chesson and Huntly, 1997). While the importance of niche differences among species during disturbance has been recognized theoretically, few studies have documented species-specific abundance patterns along disturbance gradients relative to other species and other niche axes. I collected phytoplankton and physical, chemical and disturbance data over the winter mixing period in two warm monomictic reservoirs to identify if niche differences between species are relevant during mixing, including niche axes that involve competitive processes. Warm monomictic systems circulate freely in the winter due to lack of ice cover because water temperatures do not drop below 4ºC (Wetzel, 2001). However, the intensity of mixing is variable, and can include quiescent periods, which provides a gradient on which to assess the effect of mixing intensity on the phytoplankton communities.

Second, I use the extensive phytoplankton dataset of Interlandi et al. (1999) noted above to evaluate the effect of sampling scale on the recognition of phytoplankton species abundance maxima and co-occurrence. Specifically, I artificially reduced the dataset to imitate lesser sampling intensities in order to determine the extent that sampling scale affects the recognition of phytoplankton species maxima within a lake in a single growing season, and the significance of the relationship between two species across lakes.

CHAPTER 2. Phytoplankton community dynamics during the winter destratified period in two monomictic reservoirs and the distinction between richness and dominance

INTRODUCTION

Given that a majority of lentic systems in the southern US are warm monomictic reservoirs, the paucity of published studies that include the winter circulation period is surprising. In particular, few studies are available that examine phytoplankton community dynamics during and after fall turnover (Rojo and Alvarez-Cobelas, 2001; Davies et al., 2004), however a few generalizations are available. For instance, whole-lake mixing generally decreases phytoplankton biomass due to low light availability as turbidity increases and cells are circulated deep into the water column (Wetzel, 2001). In addition, dissolved nutrient concentrations in the water column are supplemented by richer hypolimnetic waters, and can be in excess to phytoplankton growth (Sterner and Grover, 1998; Grover et al., 1999). An increase of "ruderal" species (large heavy species that rely on water column mixing to remain suspended in the water column) is associated with deep circulation or continuous mixing, while small, fast-growing species (termed "invasive" species) tend to increase with the onset of stratification (Reynolds, 1995). Beyond this, however, little is known about the spatial and temporal patterns of phytoplankton species abundance during winter circulation, and the effect of water column mixing and stability on community structure.

In addition, many studies that focus on the effect of disturbance on phytoplankton community structure in lakes examine the interruption of stratification by disturbance under the assumption that the surface layers in stable stratification most closely approximates equilibrium conditions (Sommer, 1993; Flöder and Sommer, 1999; Hambright and Zohary, 2000). However, species that are favored by mixing would be affected by the onset of stratification (Chorus and Schlag, 1993). Indeed, stratification is detrimental to many diatom species that rely on water column mixing to avoid sinking (Sherman et al., 1998; Ptacnik et al., 2003). Secondly, while some consider disturbance to function through spatial heterogeneity of resources (Sousa, 1984), mixing in lakes can

result in homogenization of the water column while stratification contributes to spatial patchiness.

Species richness has been emphasized as the primary measure of diversity in recent literature, at the expense of diversity indices (Magurran, 2004), and the presumption of interchangeability between the two has rarely been challenged (Wilsey et al., 2005). For instance, Floder and Sommer (1999) demonstrated that richness and Shannon diversity in phytoplankton communities responded similarly along a disturbance frequency gradient. However, Wilsey et al. (2005) found that the two display distinct patterns in grass communities; specifically they found that rarity (the proportion of richness contributed by rare species) and evenness (a component of diversity indices) were negatively correlated. Additionally, Smith and Knapp (2003) found that rare species contributed little to the productivity in a grassland system, and did not increase in abundance when the dominant species were removed.

I collected physical, chemical, and phytoplankton data during the winter in two monomictic reservoirs. First, I describe the patterns of these parameters during turnover and the subsequent destratified period and examine the relationship between disturbance parameters and phytoplankton dynamics. Second, I compare and contrast patterns of richness, dominance, and Simpson's diversity in the phytoplankton communities during mixing and early stratification and assess their suitability in describing community structure.

METHODS

Field sites and sample collection

Buchanan and Travis reservoirs are located on the Colorado River north and west of Austin, Texas (Figure 2.1) and are 30 and 50 m maximum depth, respectively. Buchanan is upstream of Travis, near Burnet, Texas, and a series of three small impoundments separate the two reservoirs. Turnover in both reservoirs begins approximately in October and the winter destratified period normally continues to March in Travis and April in Buchanan (Lower Colorado River Authority, unpublished data). I

collected field samples weekly to biweekly from October 2002 through March 2003 in both reservoirs, and once in each of April and May 2003. On each sampling date I collected samples for phytoplankton counts and nutrient chemistry from one primary limnetic station at 3, 12, and 21 m, and two other secondary stations at 3 m depth only. Temperature, dissolved oxygen, pH, and conductivity profiles were collected at each primary site with a calibrated Hydrolab Quanta multiparameter sonde (with depth sensor) at 3m intervals. Hydrolab parameters and nutrient chemistry samples also were collected from 3 m depth at the other sites. Photosynthetically active radiation (PAR) was measured at the primary site with a LICOR spherical light sensor at 1-m intervals to 10 m. Ambient PAR also was measured immediately above the water surface using the spherical light sensor over a black plastic oil pan used to shield light reflection from the water. Secchi depth measurements were collected at each site on each date.

Samples for nutrient chemistry were collected in 4-liter polypropylene bottles and stored on ice until processing in the laboratory. Phytoplankton samples were preserved in the field with Lugol's solution. Water for phytoplankton counts and nutrient chemistry were collected using a peristaltic pump and a hose. I tied the hose to the Hydrolab sonde to ensure samples were taken at the proper depth. Zooplankton samples were collected using a 20μm plankton net (13 cm mouth) by a vertical tow from 25-30 m to the surface and preserved in sucrose-formalin solution (Haney and Hall, 1973). I also collected zooplankton samples with an 80 μm net (50 cm mouth) after January.

Sample processing and analysis

I performed phytoplankton counts on a 10 ml subsample using a settling chamber on an inverted microscope. Small cells, including *Chrysochromulina parva* and coccoid cyanobacteria, were counted in random viewing fields in the chamber at 400x. Other small algae were counted across one strip of the chamber at 400x. Large cells and colonies, such as *Pediastrum* and *Ceratium*, were counted at 100x over the entire chamber. Phytoplankton were identified morphologically to the lowest taxon possible and mean biovolume was estimated for each species following Hillebrand et al. (1999).

Some individuals were distinguished from congenerics by morphology but not identified to species (Table 2.1).

Zooplankton samples were subdivided using a plankton splitter and organisms in the subsample were identified to order (Copepoda) or genus (Cladocera). I estimated mean dry weight for each order or genus from total length using conversions in Culver et al. (1985). In order to determine if the small net used from October through December underestimated cladoceran abundance (due to avoidance of the net during sampling), I compared the estimation of cladoceran biomass between the two nets on four dates when both nets were used. The estimate of cladoceran abundance for the large net was not consistently higher than that of the small net and so the data from the two nets were not treated differently.

Samples for chemical analysis were usually filtered within 24 hours of arrival in the laboratory and frozen if not analyzed immediately. Samples for dissolved nutrient analyses were filtered via syringe filtration through a 0.4-µm polycarbonate filters. Filtered samples for dissolved (nitrate and nitrite) N were frozen in 125-ml polypropylene bottles for later analysis. Duplicate polycarbonate filters were saved for analysis of particulate P and Si. Samples for particulate P and N analysis were filtered onto preashed GF/F filters by vacuum filtration and then frozen. I examined all filters under a dissecting microscope and removed visible zooplankton before freezing.
Dissolved inorganic nitrogen (DIN) was reduced to nitrite using reagents from a Nitrate Nitrogen Low Range Test Kit (Hach, Inc.) and measured on a Spectronic 20 Genesys spectrophotometer at 509 nm. Ammonia-nitrogen was not measured because previous analyses at the surface show concentrations below the detection limit in both reservoirs during the winter (Lower Colorado River Authority, unpublished data), therefore DIN may be minimally underestimated in this study. Soluble reactive phosphorus (SRP) was measured by the ascorbic acid method of Strickland and Parsons (1972) modified by U. Sommer (J.P. Grover, personal communication). Soluble reactive Si (SRSi) was measured by the molybdosilicate method (APHA, 1998). Particulate N and C were measured by combustion and gas chromatography on a Carlo Erba 1106 in the laboratory

of S.S. Kilham at Drexel University. Samples for particulate P were digested using persulfate digestion and analyzed as soluble reactive phosphorus as above. Many samples were contaminated with an unknown source of phosphorus during processing and were excluded from the analysis. Samples for biogenic Si analysis were digested following Franck et al., (2000) and dissolved Si was measured as above. Several samples were analyzed for biogenic Si and all were below detection limit so the analysis was halted and the results will not be presented here (an analysis with a dilution series of a *Cyclotella bodanica* culture was successful).

Quantification of disturbance

Disturbance was quantified using the following indices or parameters:

1. The number of hours in which wind speeds exceeded 3.5 ms^{-1} over the seven days prior to the sampling date (windy hours). Initial examination of the data demonstrated that this wind speed and time interval resulted in the strongest correlation with phytoplankton biomass. Data were obtained from the University of Texas Applied Researched Laboratories weather station on Travis and from the National Weather Service stations in Burnet and Georgetown, Texas for Buchanan.

2. Light extinction coefficient (k). The extinction coefficient is a measure of the absorption and attenuation of surface light through depth by dissolved and particulate materials suspended in the water column (Wetzel, 2001). During the winter, most of the light extinction is due to abiotic materials. k was calculated from the exponential decay curve through the light profile using CurveExpert 1.3 (© Daniel Hyams), where

$$I_z = ae^{-kz}$$

I_z is the irradiance at depth z and a is the y-intercept of the curve.

3. River inflow rates. Inflow rates for Travis were the sum of the release rates for Starcke dam upstream of the reservoir (Lower Colorado River Authority, unpublished data) and the discharge rates measured on the Pedernales River near Johnson City, Texas (United States Geological Survey, unpublished data). The Pedernales River is a major tributary into Travis. Inflow rates for Buchanan were estimated from the discharge of the

Colorado River near San Saba, Texas (United States Geological Survey, unpublished data).

4. Crustacean zooplankton biomass. Crustacean zooplankton are the primary grazers in freshwater pelagic systems.

Data analysis

Diversity was calculated by a modified Simpson's index (Interlandi and Kilham, 2001) with biovolume as a surrogate for species abundance:

$$\text{Diversity} = 1 / \Sigma p_i^2$$

where p is the percentage of total community biomass for an individual species (i). A species was considered dominant if its biovolume comprised at least 10% of the total phytoplankton community biovolume. A species was considered rare if it comprised less than 2.5% of the total biovolume. Species richness was estimated as the number of species counted in a sample, therefore it is bounded by the detection limit of one cell per 10 ml for large taxa or per 0.03 ml for small taxa. Species rank/abundance plots were derived for several dates in both reservoirs following Magurran (2004).

Spearman rank order correlation analysis between total phytoplankton biovolume and disturbance parameters was conducted on SYSTAT 10 (Systat, Inc.). Ruderal (r) and invasive (c) species were identified using surface area to volume ratio and maximum linear dimension following Reynolds (1995).

Light meter data were not taken on four sampling dates due to variable cloud cover. On those dates, I estimated the extinction coefficient by fitting a regression between the extinction coefficient and Secchi disk depth on the other sampling dates. In Travis, the extinction coefficients on January 9 and February 11 were estimated by the logarithmic equation:

$$k = 1.42e^{-0.334\text{Secchi}}$$

and in Buchanan, by a linear relationship:

$$k = 1.22 - 0.255\text{Secchi}$$

where Secchi is the Secchi disk depth in m.

RESULTS

Winter destratified period

Deepening and weakening of the summer thermocline (turnover) was already in process on the first sampling date in both reservoirs and continued through the end of October. In Travis, the extinction coefficient increased during turnover and the subsequent destratified period until late January then decreased well before stable stratification, while in Buchanan the extinction coefficient was erratic and variable (Figure 2.2). The mean water temperature at 3m was similar in the two reservoirs. Total algal abundance (biovolume) declined precipitously throughout turnover in Travis, and declined except for a 3-week period in Buchanan (Figure 2.3). Abundance then remained relatively low in both reservoirs until stratification (except for one surface bloom of *Aphanizomenon flos-aquae* that was not captured by the 3m samples in Buchanan on January 28). Biovolume in Buchanan was consistently twice or more than that of Travis until March, when Travis formed stable stratification before Buchanan.

Soluble reactive phosphorus (SRP) increased from October to its peak in December in both reservoirs, and then generally decreased through the remainder of the sampling period, well before stable stratification (Figure 2.4). While the SRP concentrations appear similar in the reservoirs, phytoplankton biomass in Buchanan was normally twice or more than the biomass in Travis, therefore uptake rates in Buchanan were likely substantially higher and the two concentrations are not comparable. Dissolved inorganic nitrogen (DIN) similarly increased in both reservoirs at the beginning of the destratified period but peaked in Travis in January, and did not peak in Buchanan until March. Soluble reactive silica (SRSi) was consistently higher in Travis than Buchanan (Figure 2.5) and dropped in Buchanan after stable stratification and an increase in the diatom species *Fragilaria crotonensis*. The drop in SRSi concentration in Travis on 20 December was not accompanied by a strong increase in diatom abundance and was not preceded an increase in river inflow volume, therefore it is possible this decrease was laboratory error.

The mean particulate C:P and C:N ratios in Travis during the destratified period were 46.3 and 6.8, respectively, with maximum values of 76.9 and 7.8. The mean particulate C:P and C:N ratios in Buchanan were 58.2 and 6.4, with maximum values of 102.2 and 7.4. The particulate nutrient ratios in both reservoirs were below the minimum predicted for moderate limitation of nitrogen and phosphorus (129 for C:P and 8.3 for C:N; Hecky et al., 1993). Detrital influence has been shown to increase particulate C:P and C:N ratios (Hecky et al., 1993; Hessen et al., 2003).

Flagellates dominated the phytoplankton community through the winter destratified period, in particular the cryptomonad species *Campylomonas rostratiformis* and *Cryptomonas phaseolus* (Table 2.1). In Travis, ruderal species were highest for a brief time during turnover, then maintained low abundances during the destratified period and disappeared at the beginning of stratification (Figure 2.6). In Buchanan, ruderal species showed a similar pattern, but exhibited the highest abundance after stratification (Figure 2.6). The diatom *Fragilaria crotonensis* dominated the phytoplankton community in Buchanan after stratification, suggesting that its classification as a ruderal species (Reynolds, 1995) due to sensitivity to stratification (Reynolds, 2002) may be invalid.

The abundance of *C. rostratiformis* and *C. phaseolus* was conspicuously heterogeneous across depths throughout the winter destratified period in Buchanan (Figure 2.7), and in late January and February in Travis (Figure 2.8). The differentiation occurred when surface warming resulted in as little as 0.02°C change across 1 m depth.

Total algal biovolume was strongly and significantly related to light availability in Travis, while in Buchanan, the extinction coefficient was not significantly correlated to algal biovolume (Table 2.2, Figure 2.9). Rather, in Buchanan, total algal biovolume was negatively related to the number of windy hours from a northeast direction (Table 2.2, Figure 2.9). However, the drop in abundance due to wind was not attributable to an increase in the extinction coefficient (Table 2.2). Wind did not significantly affect algal biovolume or the extinction coefficient in Travis. These results are consistent with my observations in the field that Buchanan was frequently turbulent at the surface in

response to wind, and on two occasions prevented me from sampling, while Travis was rarely so. River discharge into the reservoirs was not related to algal abundance or the extinction coefficient. Zooplankton biomass was extremely low in Travis (Figure 2.10) and was not related to algal abundance (Table 2.2). Zooplankton biomass was much higher in Buchanan and its correlation to algal abundance was negative although not significant (Figure 2.10, Table 2.2). The abundance of the dominant species in Buchanan, *C. rostratiformis*, was negatively related to calanoid copepod density (data not shown).

Community diversity and dominance

Species richness in Travis was high during turnover, gradually decreased through stratification, and then increased again in May (Figure 2.11). The drop in richness between 28 February and 21 March was due to the disappearance of several diatom species that presumably settled out of the water column as the reservoir stabilized and stratified. The richness in May was similar to that measured in June and August of 2001 (22 and 20, respectively; Bowles, unpublished data). Simpson's diversity was variable, but generally higher during the destratified period after turnover. Diversity decreased in late January and approximated the number of dominant species as the water column stabilized.

Species richness in Buchanan was consistently higher than that of Travis throughout the destratified period (Figure 2.11). The number of species in Buchanan increased substantially at the end of January and remained high through May. Richness in May exceeded that measured in June and August of 2001 (27 and 28, respectively). The 28 January collection date was preceded by 54 windy hours over the prior seven days and this likely precipitated strong mixing similar to turnover. Large diatom species known to rely on water column mixing increased after this date. Simpson's diversity was highly variable throughout the winter and dropped dramatically on dates in which the dominant species accounted for a large proportion of the biovolume. As in Travis, diversity in Buchanan approximated the number of dominant species after stratification.

Despite the higher species richness in Buchanan, the species rank/abundance curves progressed similarly in the two reservoirs over time, where richness and evenness were higher during turnover to early January (Figure 2.12).

The proportion of phytoplankton biovolume contributed by rare species declined throughout the winter in Travis and Buchanan to less than 10% in May (Figure 2.13). Conversely, the contribution of rare species to richness remained fairly steady and was approximately 80% in both reservoirs in May.

DISCUSSION

Winter destratified period

The first task of this study was to understand the spatial and temporal extent of disturbance through the winter destratified period and its effect on phytoplankton community characteristics. One of the surprising results was that winter 'mixing' in these monomictic reservoirs may be a misnomer given they were heterogeneous over space and time during the winter. First, the abundance of the dominant flagellates was heterogeneous across depth in both reservoirs well before stable stratification and when the water column temperature gradient was approximately 0.2ºC per m. This suggests that much less than stable seasonal stratification prevents whole-lake circulation and also suggests a difference in circulation intensity between turnover and the subsequent destratified period. This may have contributed to the drop in ruderal species after turnover in both reservoirs. Indeed, weak vertical mixing in the absence of water column stability can contribute to phytoplankton blooms (Townsend et al., 1992). Secondly, SRP concentrations in the water column declined well before stable stratification. This was similarly described by Sterner (1994). SRP loss can occur through algal uptake, bacterial uptake (Vadstein et al., 1993) and adsorption to calcium carbonate (House and Donaldson, 1986). However, the decline of SRP in Travis accelerated after the onset of water column stability, decrease in the extinction coefficient and concomitant increase in phytoplankton abundance, indicating that algal uptake was a primary factor in that reservoir.

Heterogeneity of water temperature and algal abundance across depth occurred throughout the destratified period in Buchanan, but did not begin in Travis after turnover until late January. Winter temperature dynamics in Travis appear to be consistent with convective mixing, where circulation in the water column continues until it reaches an isothermal minimum regulated by air temperature (Wetzel, 2001). Indeed, water column stability in Travis (indicated by a small temperature gradient across depth) began after the water temperature dropped below that of the average minimum air temperature. Conversely, the few instances in which the water column was homogenous after turnover in Buchanan were likely aided wind-driven mixing, rather than convective circulation alone. The cause of reduced influence of convective mixing in Buchanan relative to Travis is unclear, but may be associated with total lake volume (Wetzel, 2001).

The strong relationship between the extinction coefficient and phytoplankton biovolume in Travis, and between wind-induced mixing and biovolume in Buchanan, supports the widely-held assumption that the decline of algal biomass in lakes during the winter months is due to light limitation (e.g., Sommer, 1985; Gibbs and Vant, 1997; Vincent, 1983) from deep mixing and high abiotic turbidity. The dominance of cryptomonads is common in the winter (e.g. Barone and Naselli-Flores, 2003) even under ice cover (Danilov and Ekelund, 2001; Phillips and Fawley, 2002) and can be attributed to their tolerance of low light (Kugrens and Clay, 2003).

Community diversity and dominance

Species richness, Simpson's diversity index, and the number of dominant species exhibited distinct, and sometimes opposing, patterns during the winter in Travis and Buchanan, suggesting each should be considered separately when investigating the effects of disturbance. Simpson's diversity has been used as a proxy for richness to evaluate the effects of resource competition on phytoplankton communities (Interlandi and Kilham, 2001; Grover and Chrzanowski, 2004) because it emphasizes dominant species. This is important in natural phytoplankton communities where dominants consume the bulk of the resources, but rare species are always present due to perpetual nonequilibrium (Interlandi and Kilham, 2001). Indeed, in this study Simpson's diversity

approximated the number of dominant species after stratification in both lakes. However, during the winter destratified period the index dropped dramatically in response to small increases in the abundance of the dominant species relative to other species during periods of mild water column stability. For this reason, rank/abundance plots are recommended over diversity indices as a means to examine richness and evenness following disturbance or during succession (Magurran, 2004).

Species richness during the winter in both reservoirs was dominated by the presence of rare species, and this did not change after stratification. Conversely, the contribution to total biomass by rare species never exceeded 20% in either reservoir and declined further when the dominant species were favored by water column stability. The recent emphasis on richness as a measure of diversity may be inappropriate for phytoplankton, as recently argued for grasses (Wilsey et al., 2005), because it assumes equality among the species. For instance, investigations into mechanisms of coexistence between species explore the cause of the failure of the dominant species, which possesses higher "fitness" for the environmental conditions and demands the most resources, to competitively eliminate all other species (Chesson, 2000). Rare species, while important to conservation concerns, are minimally relevant to questions of coexistence because they are not the primary drivers of nutrient availability (Smith and Knapp, 2003).

Buchanan and Travis reservoirs were selected for this study in part because of their broad differences in productivity. Summer phytoplankton biomass (measured as chlorophyll *a*) is consistently twice or more in Buchanan than Travis (Lower Colorado River Authority, unpublished data). In addition, in this study winter zooplankton abundance in Buchanan exceeded Travis on every sample date. However, phytoplankton biomass decreased in both reservoirs during turnover and remained low during the subsequent destratified period primarily due to low light. Periods of calm weather in Buchanan, and the termination of convective mixing in Travis, allowed phytoplankton growth near the surface and contributed to spatial heterogeneity of abundance well before stable stratification and while the water temperatures were at the winter minimum. This contributed to the steady decline of soluble reactive phosphorus during the destratified

period in both reservoirs. Clearly, monomictic reservoirs undergoing winter circulation are dynamic and far from homogenous. This study also demonstrates that species richness cannot be used interchangeably with diversity indices during disturbance, and moreover that neither may be appropriate when community succession is of interest. This is particularly relevant to studies that investigate the effect of disturbance on community structure, such as those testing the Intermediate Disturbance Hypothesis (Connell, 1978).

Table 2.1. Phytoplankton taxa collected from Travis and Buchanan reservoirs from October 2002 through May 2003. "+++" = 10% of the total biovolume in any sample, "++" = 2.5% of the total biovolume in any sample, "+" = less than 2.5% of the biovolume in all samples, "0" = was not detected in the reservoir. r = ruderal species, i = invasive species. Unkn. = unable to identify to genus, spp. = contains two or more distinct forms that were not identified to species.

Taxa	Travis	Buchanan	Taxa	Travis	Buchanan
Green algae			Diatoms		
Carteria sp.	+++	+++	*Nitzschia* spp.	+++	+++
Unkn. green flagellate	+++	+++	*Anomoneis* sp.	++	++
Unkn. green coccoid	+++	+++	*Navicula* spp.	+	0
Staurastrum spp. (r)	+++	++	*Synedra tenera*	++	++
Cosmarium spp.	+	+	*Achnanthidium minutissimum* (c)	+	+
Pediastrum spp. (r)	++	++			
Tetraedron sp. (c)	+++	+++	*Achnanthes* sp. (c)	++	+
Crucigenia sp. (c)	++	++	Unkn. cymbelloid	+	0
Oocystis sp.	++	+++	*Gomphonema* sp.	+	0
Scenedesmus spp.	++	++	*Cyclotella ocellata* (c)	++	+++
Mougeotia sp.	+++	+++	*C. meneghiniana* (c)	+	++
Quadrigula sp.	+	+	*Thalassiosira pseudonana* (c)[1]	+	+
Kirchneriella sp.	+	+			
Closterium spp. (r)	+	+++	*Stephanodiscus hanzschii* (c)	++	+
Phacus sp.	+	+			
Coelastrum sp.	+++	++	*S. minutulus* (c)	+	+
Lagerheimia sp.	+	++	*S. agassizensis* (c)	++	+++
Pteromonas sp.	+	0	*Fragilaria crotonensis* (c)	++	+++
Shroederia sp.	+	+			
Eudorina sp.	+++	0	*Aulacoseira granulata* (r)	++	+++
Dictyosphaerium sp.	0	+			
Sphaerocystis sp.	0	++	*A. cf. distans* (c)	0	+++
			Melosira varians	+++	+
Cyanobacteria			Chrysophytes		
Unkn. bluegreen filament	+++	+++	*Dinobryon* sp.	+	+
Aphanizomenon flos-aquae	+	+++			
Lyngbya sp.	+	0			
Unkn. bluegreen coccoid	+++	++			
Raphidiopsis sp.	+++	+++			
Merismopedia sp.	+	+			
Anabaena spp.	+	+++			
Gomphosphaeria sp.	0	+			
Cryptomonads					
Cryptomonas phaseolus	+++	+++			
Campylomonas rostratiformis	+++	+++			
Plagioselmis nanoplanctica (c)	+++	+++			
Dinoflagellates					
Peridinium sp.	+++	+++			
Ceratium hirudinella	++	++			
Prymnesiophyes					
Chrysochromulina parva (c)	+++	+++			

[1] Includes small *Cyclotella pseudostelligera*

Table 2.2. Spearman rank correlations between disturbance parameters and algal abundance in Travis and Buchanan reservoirs during the winter destratified period. Total algal biovolume is the mean total biovolume across samples taken on each date. Change in algal biovolume from the prior sampling date was used in evaluating the relationship to windy hours and discharge. The fetch of Travis and Buchanan reservoirs is approximately northwest and northeast, respectively. Significance was evaluated at $p<0.05$. na = relationship was not assessed

Travis (n=14)	Total algal biovolume ($\mu m^3 ml^{-1}$) or change in algal biovolume (%)	Extinction coefficient
Extinction coefficient	-0.855 ($p<0.001$)	
Zooplankton biomass ($\mu g ml^{-1}$)	0.279	na
No. hours NW wind >3.5 ms^{-1} over 7 days	-0.169	-0.371
River discharge (cfs)	-0.046	0.121
Buchanan (n=14)		
Extinction coefficient	-0.191	
Zooplankton biomass ($\mu g ml^{-1}$)	-0.292	na
No. hours NE wind >3.5 ms^{-1} over 7 days	-0.626 ($p=0.02$)	-0.103
River discharge (cfs)	-0.165	0.310

Figure 2.1. Highland Lake reservoir series, Texas. Map courtesy of the Lower Colorado River Authority.

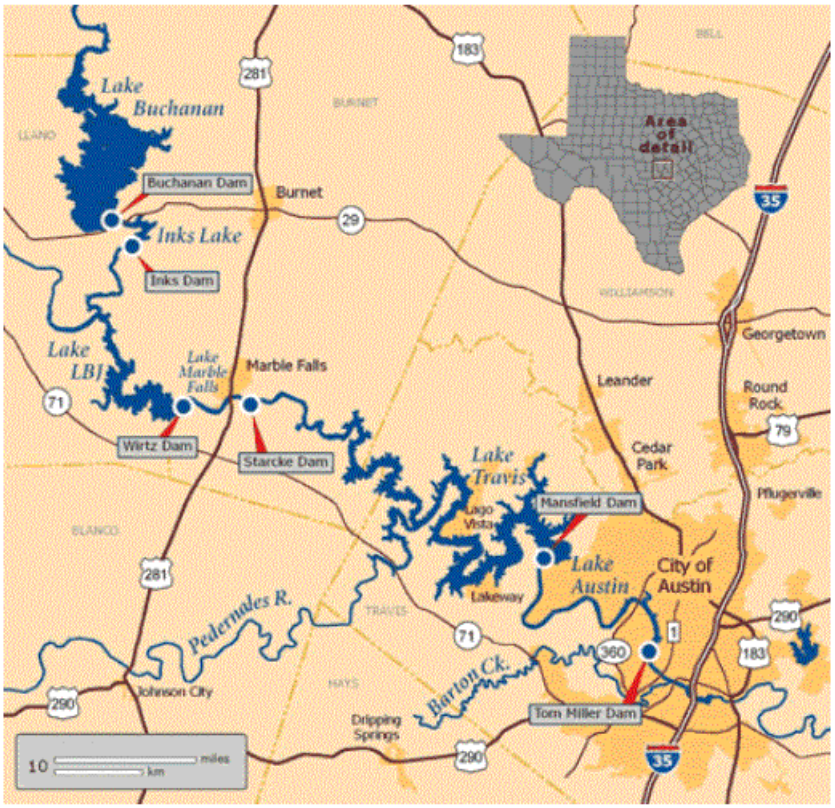


Figure 2.2. Extinction coefficient (A) and water temperature at 3m (B) in Travis and Buchanan reservoirs from October 2002 through May 2003. The arrows represent the approximate end of the destratified period in Travis (closed triangle) and Buchanan (open triangle).

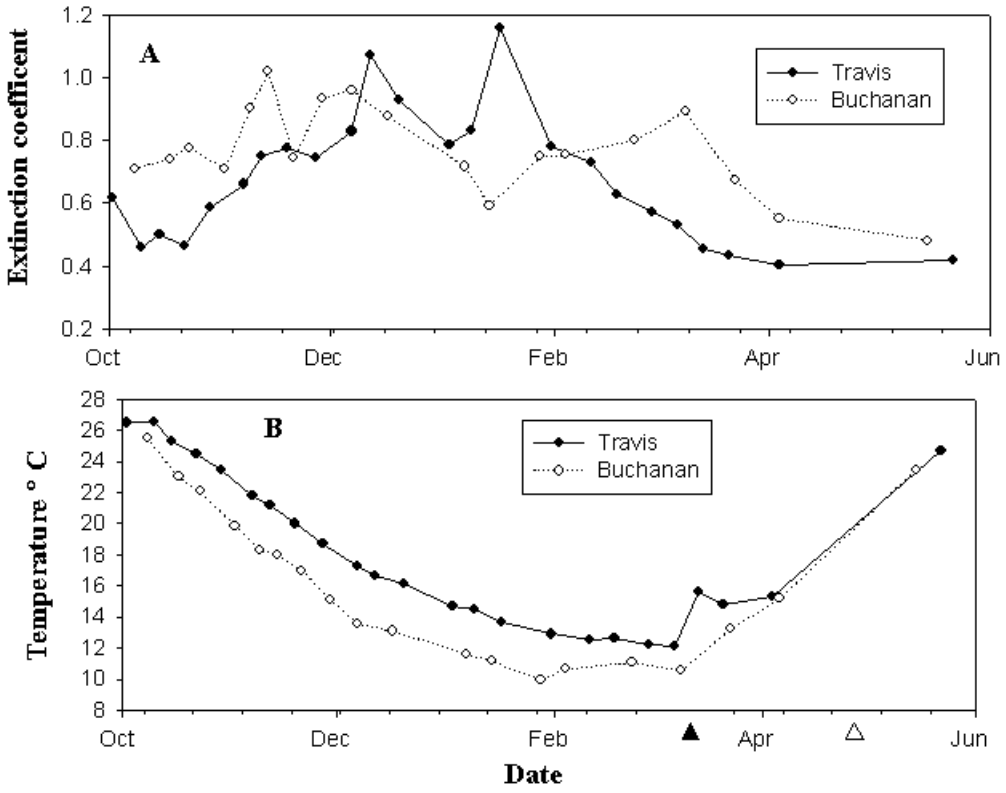


Figure 2.3. Mean total algal biovolume across samples taken from Travis and Buchanan reservoirs (error bars are ± 1 SE). Samples were taken from 3, 12, and 21m depths at the primary sample site and at 3m depth at two other sites. In Buchanan, the 21m samples were not collected on 14 November, 7 December and 23 February due to windy conditions. The arrows represent the approximate end of the destratified period in Travis (closed triangle) and Buchanan (open triangle). The * indicates the date of a surface bloom of Aphanizomenon flos-aquae in Buchanan that was not captured in the 3m samples.

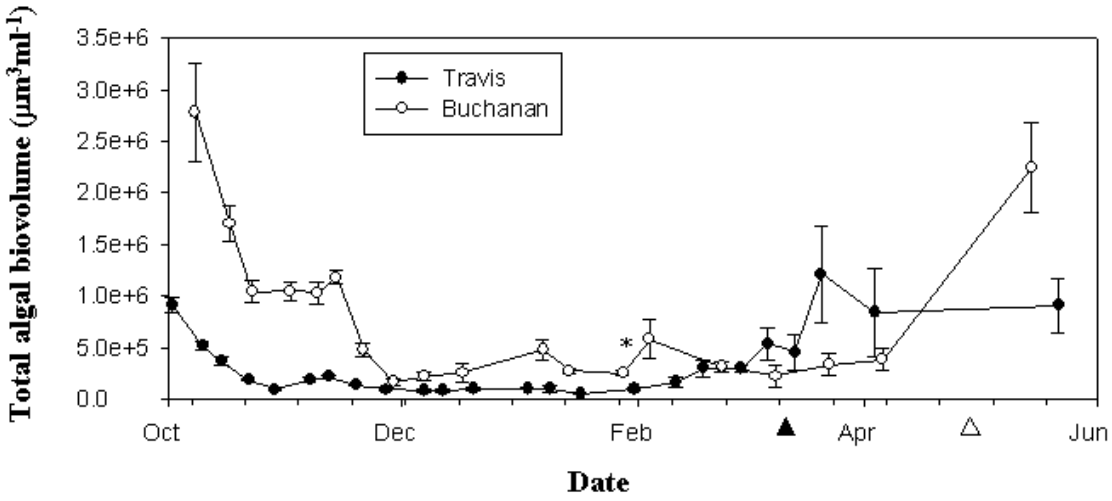


Figure 2.4. Mean soluble reactive phosphorus (SRP) and dissolved inorganic nitrogen (DIN) levels across samples from Travis and Buchanan reservoirs. Depths of samples used to calculate the means as in Fig. 2.3. The arrows represent the approximate end of the destratified period in Travis (closed triangle) and Buchanan (open triangle). Error bars are ± 1 SE.

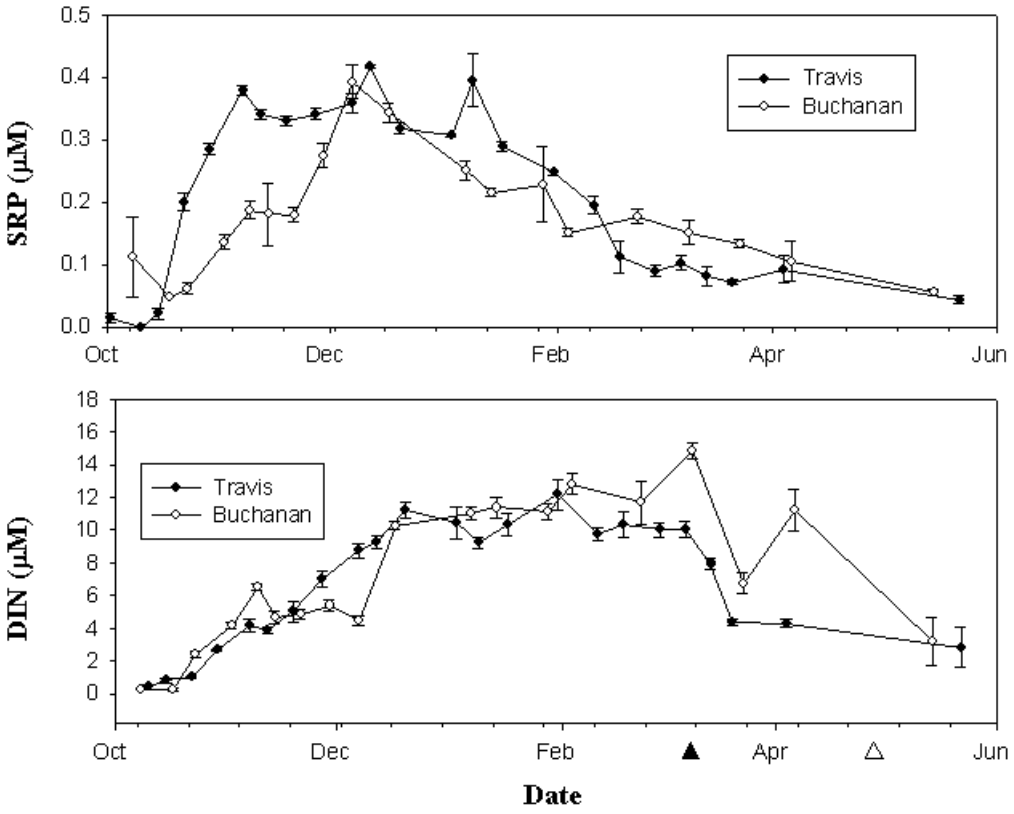


Figure 2.5. Mean soluble reactive silica (SRSi) levels across samples from Travis and Buchanan reservoirs. Depths of samples used to calculate the means as in Fig. 2.3. The arrows represent the approximate end of the destratified period in Travis (closed triangle) and Buchanan (open triangle). Error bars are ± 1 SE.

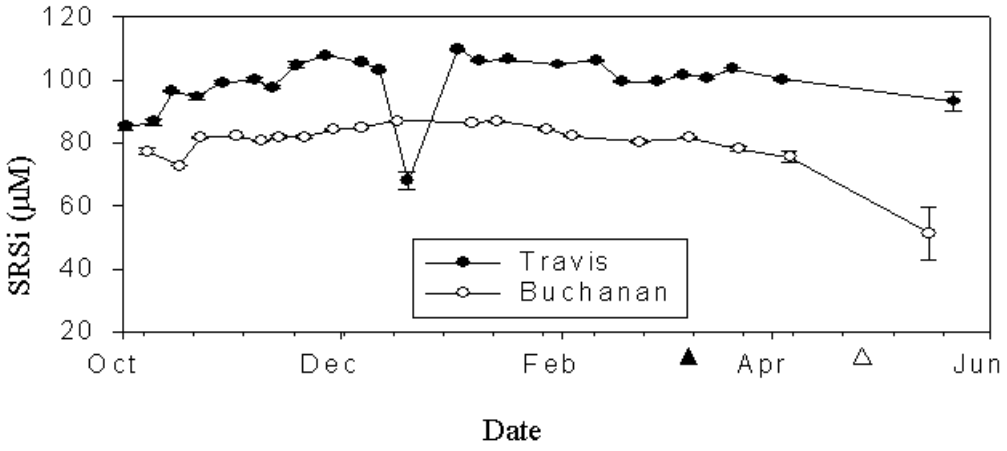


Figure 2.6. Percentage of total algal biovolume contributed by ruderal species and invasive species (Reynolds, 1995) across samples in Travis (A) and Buchanan (B) reservoirs between October 2002 and May 2003. The arrows represent the approximate end of the destratified period in Travis (closed triangle) and Buchanan (open triangle).

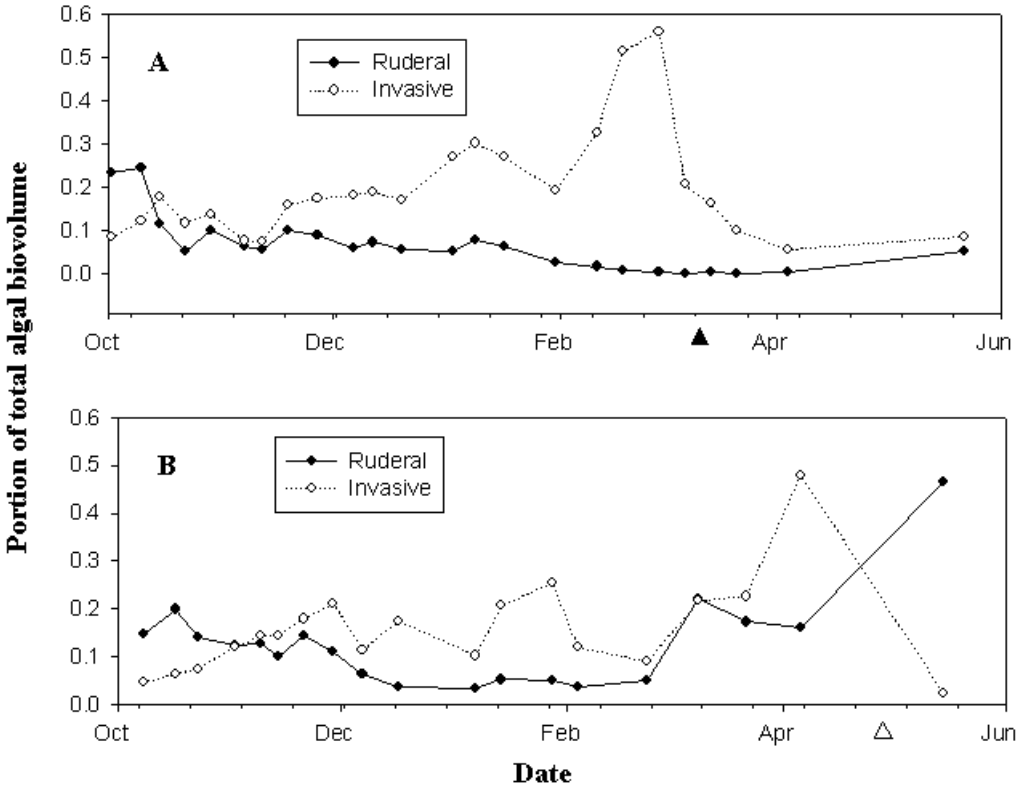


Figure 2.7. Abundance of *Cryptomonas phaseolus* in Travis reservoir at 3, 12, and 21m depths, and temperature profiles to 30 meters depth during the winter destratified period from October 2002 to February 2003.

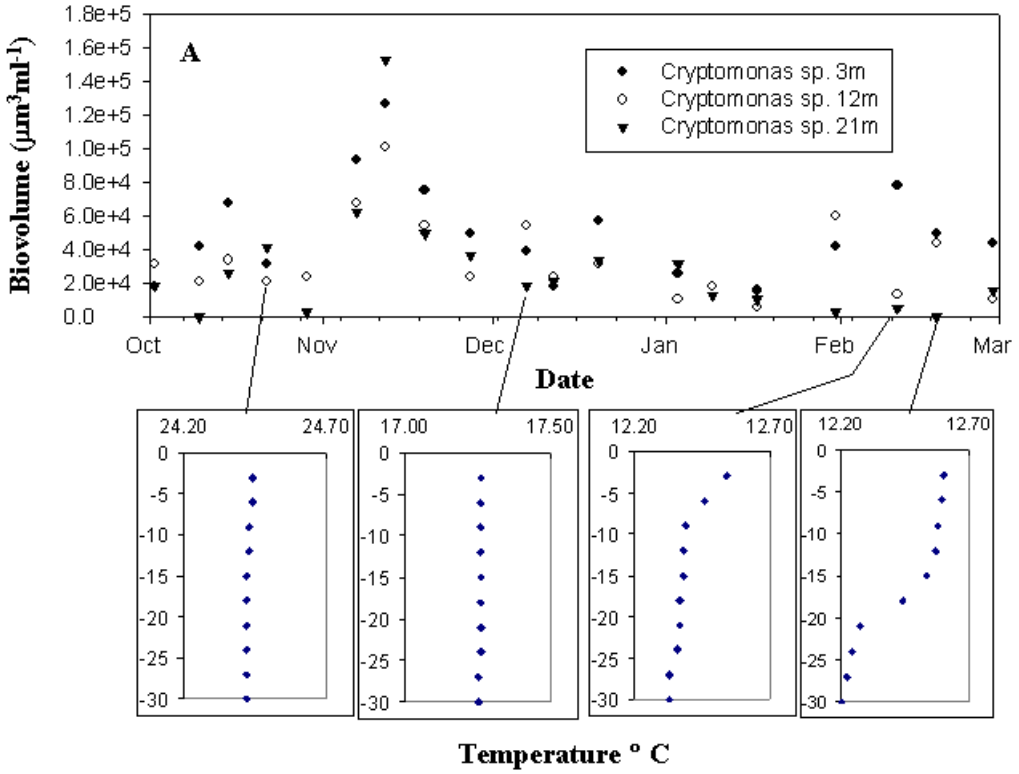


Figure 2.8. Abundance of *Campylomonas rostratiformis* in Buchanan reservoir at 3, 12, and 21m depths, and temperature profiles to 30 meters depth during the winter destratified period from October 2002 to March 2003. The deepest samples collected in Buchanan on 14 November and 7 December were from 18m, and were not collected on 23 February due to windy conditions.

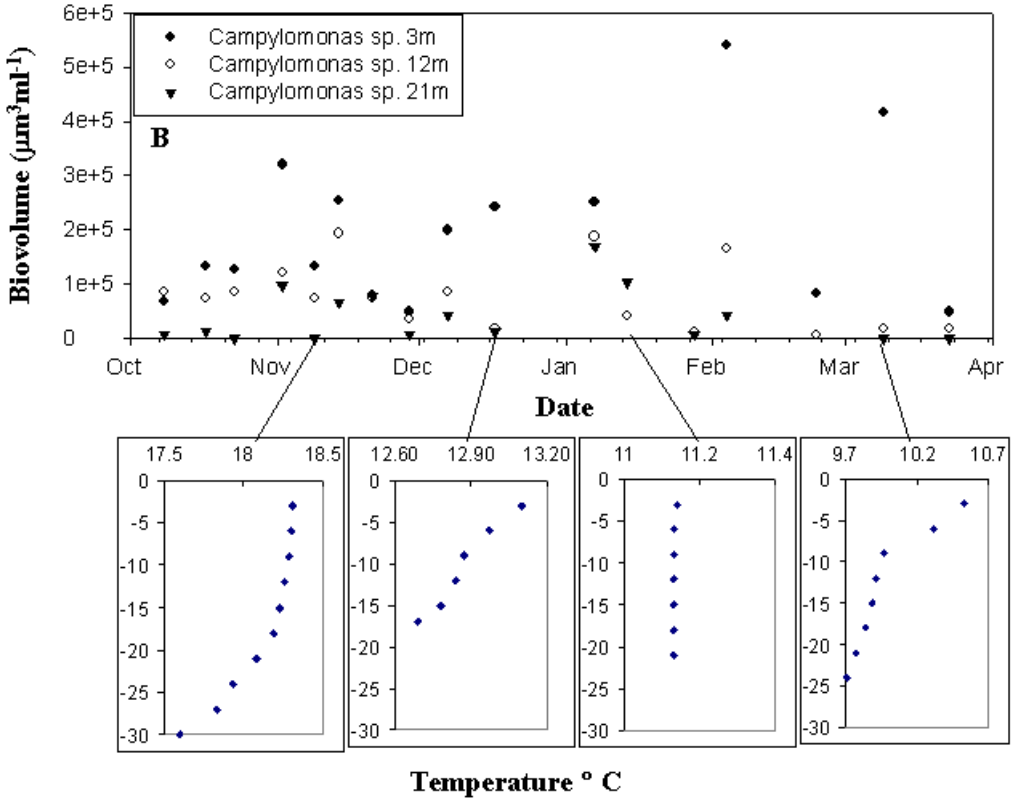


Figure 2.9. Correlations between the extinction coefficient and total phytoplankton biovolume, and between the number of windy hours and the proportion change in phytoplankton biovolume from the prior sample date during the winter destratified period in Travis (A) and Buchanan (B) reservoirs. Data were collected from November 2002 through February 2003 in Travis and through March 2003 in Buchanan. Phytoplankton biovolume measures are the mean of samples as in Figure 2.3. The number of windy hours was estimated as the number of hours when wind speeds exceeded 3.5 m s-1 in the direction of the fetch of the reservoir (NW in Travis and NE in Buchanan).

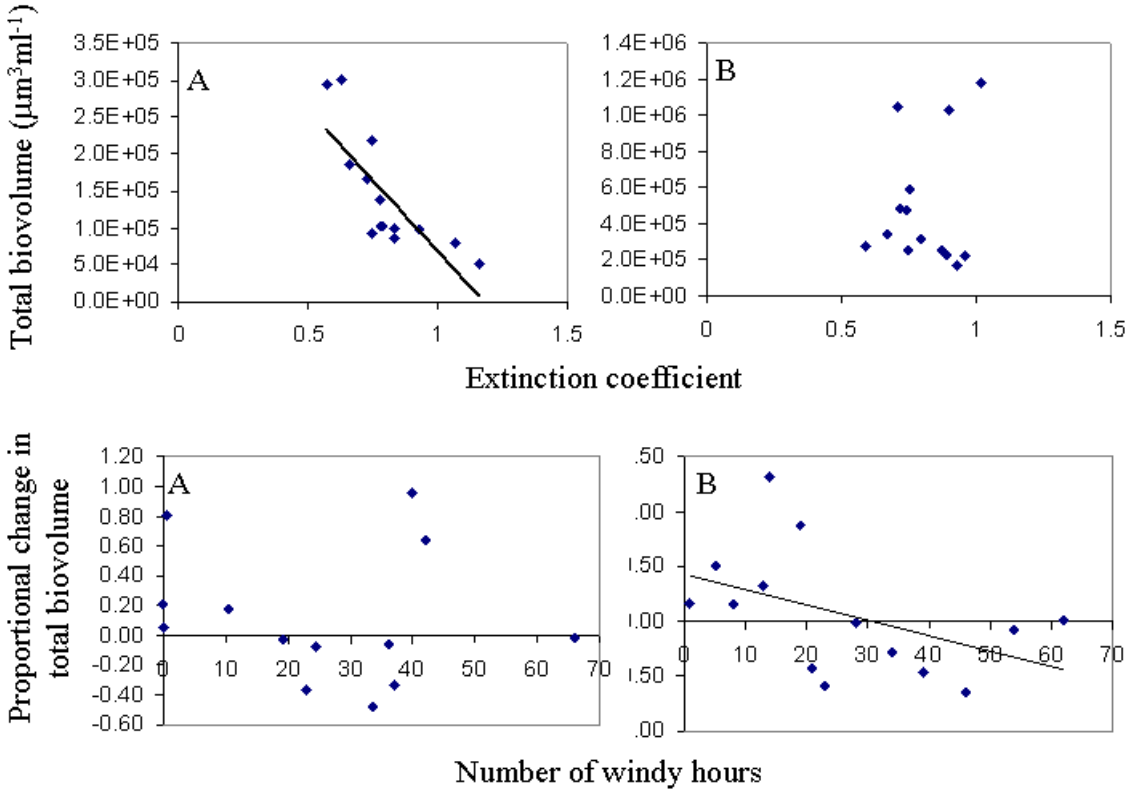


Figure 2.10. Zooplankton biomass in Travis and Buchanan Reservoirs during the destratified period from November 2002 through February 2003 in Travis and March 2003 in Buchanan.

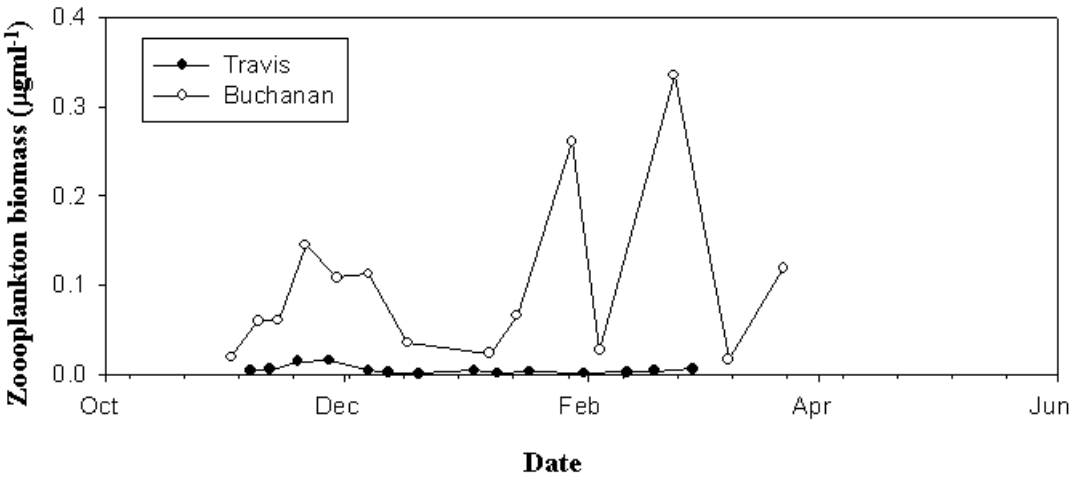


Figure 2.11. Simpson's diversity index, number of dominant species, and species richness in Travis (A) and Buchanan (B) reservoirs from October 2002 to May 2003. Values are the mean of three samples collected at 3m depth in each reservoir. The arrows represent the approximate end of the destratified period in Travis (closed triangle) and Buchanan (open triangle).

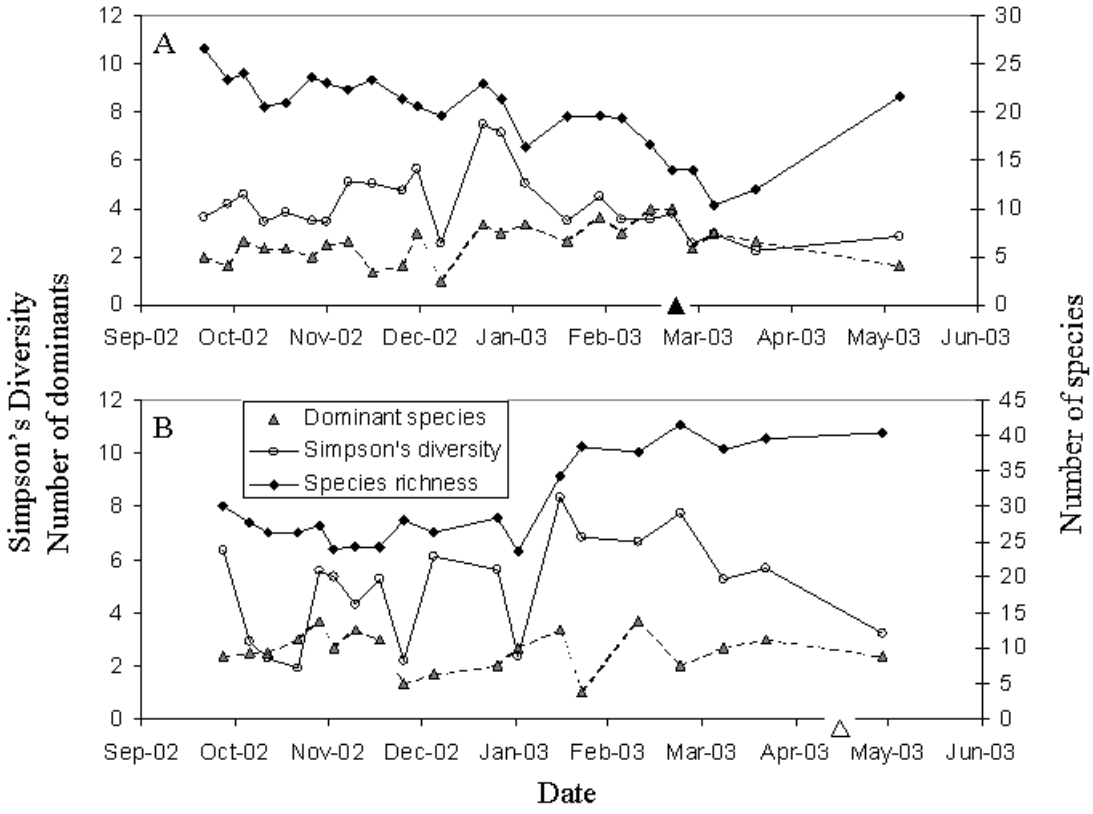


Figure 2.12. Rank/abundance curves for selected dates in Travis (A) and Buchanan (B) reservoirs from October 2002 to May 2003. Samples were collected at the primary sample sites at 3m depth.

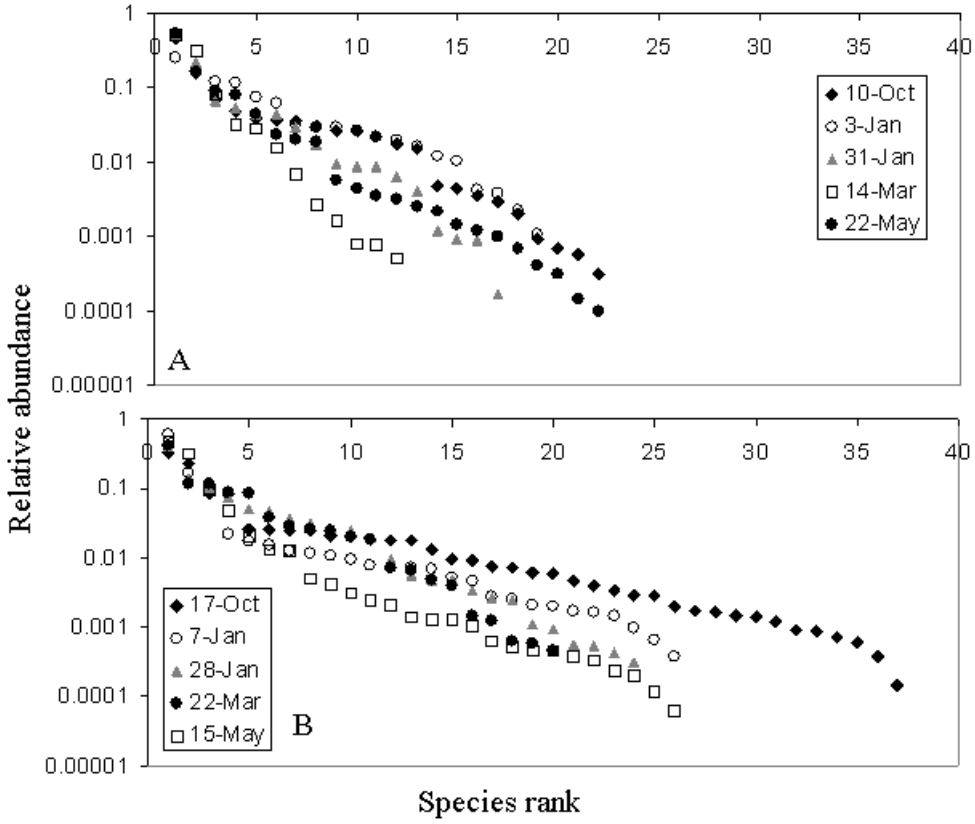
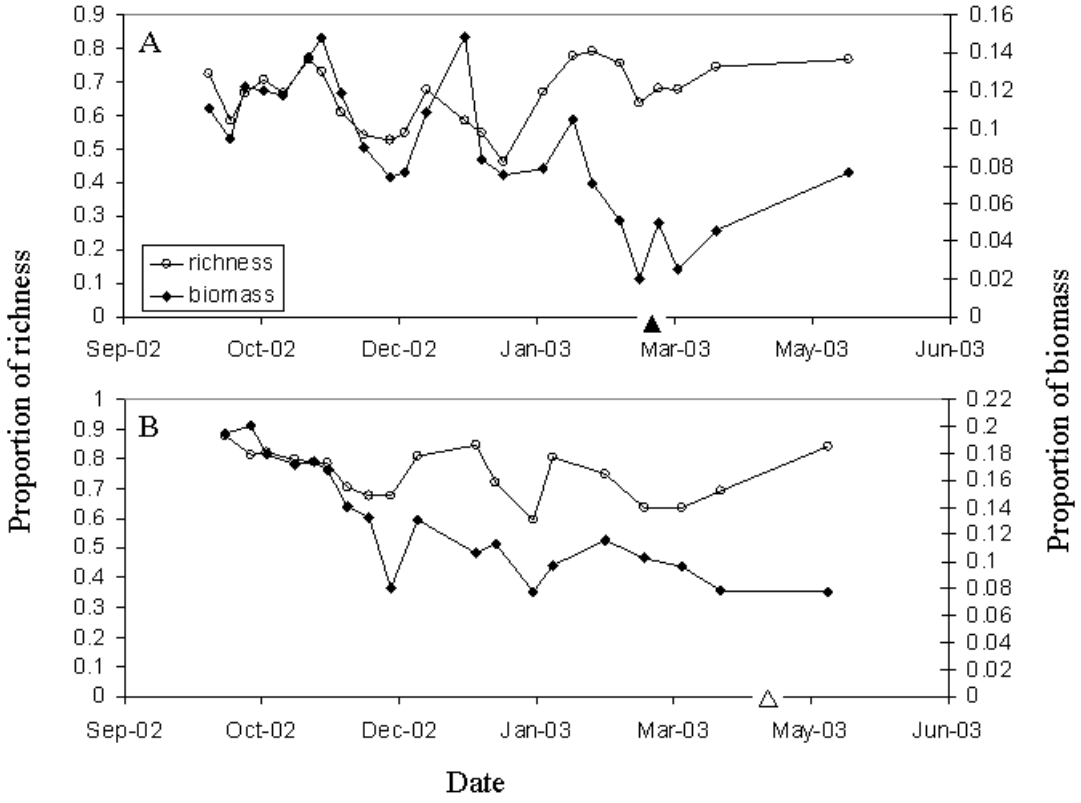


Figure 2.13. Contribution of rare species to species richness and total phytoplankton biomass in Travis (A) and Buchanan (B) reservoirs from October 2002 to May 2003. Values are the mean of three samples collected at 3m depth in each reservoir. The arrows represent the approximate end of the destratified period in Travis (closed triangle) and Buchanan (open triangle).



CHAPTER 3. Niche differences versus neutral dynamics among phytoplankton species during mixing.

INTRODUCTION

Since the pioneering work by Hutchinson (1961, 1967) phytoplankton species have been used as model systems to generate ecological theory, most notably in the examination of competitive processes and their effect on diversity and coexistence (Tilman et al., 1982; Grover, 1997; Leibold, 1999). Among these is resource competition theory, which demonstrated that trade-offs in resource requirements among competing species allow co-existence (Tilman et al., 1982). Trade-offs form the basis of niche differences among species, and occur when a species possesses a trait that enhances its ability to perform one function but unavoidably decreases its ability to perform another (Chase and Leibold, 2003).

Niche theory not only considers resource requirements but also morphological and physiological differences between species that can affect relative susceptibility to predation and tolerance to stress (Chase and Leibold, 2003). For instance, Hutchinson (1967) evoked disturbance as an explanation for high diversity in phytoplankton under the assumption that environmental variability prevented competitive exclusion. However, theory predicts that non-equilibrium conditions do not necessarily preclude competitive processes (Chesson and Huntly, 1997) because physiological trade-offs can occur between tolerance to stress and competitive ability (Chase and Leibold, 2003). While the importance of niche differences among species during disturbance has been recognized theoretically, few studies have documented species-specific abundance patterns along disturbance gradients relative to other species and other niche axes.

Recently, neutral theory (Hubbell, 2001, 2005) challenged the relevance of functional distinctiveness among species in structuring communities because it presumes that species abundance patterns are a result of stochastic processes, such as probabilistic species replacement and random mortality, rather than species-specific responses to environmental parameters. In this sense, neutral theory is not unlike the use functional

groups (Hubbell, 2005), where differences among species within groups, particularly in regard to competitive ability, are ignored.

I examined the phytoplankton communities in two warm monomictic reservoirs at a fine sampling scale during winter circulation to identify if niche differences between species are relevant during mixing, including niche axes that involve competitive processes. Warm monomictic systems circulate freely in the winter due to lack of ice cover because water temperatures do not drop below 4ºC (Wetzel, 2001). However, the intensity of mixing is variable, and can include quiescent periods, which provides a gradient on which to assess the effect of mixing intensity on the phytoplankton communities. The reservoirs are connected by the main stem of a river system and differ in productivity levels and exposure to wind (Bowles, Chapter 2, this volume). Therefore, their phytoplankton communities are derived from the same species pool, but populations of individual species are subject to local environmental conditions. Canonical correspondence analysis was used to identify relevant ecological parameters in both reservoirs in this study. The relative abundance of selected co-occurring species was then compared along ecological gradients against the predictions of neutral theory (Hubbell, 2001, 2005). Neutral theory assumes that species are functionally equivalent at the local scale, and predicts that changes in species abundance through time are due to stochastic processes and are unrelated to environmental gradients (Hubbell, 2001; Holyoak et al., 2005). For this reason, it is considered the opposite of niche theory (Chase and Leibold, 2003) and is suggested as a null model to evaluate niche-based models of community processes (Holyoak et al., 2005).

METHODS

Buchanan and Travis reservoirs are the first and fifth reservoirs in the Highland Lakes on the Colorado River north and west of Austin, Texas. I collected phytoplankton samples, physical and chemical parameters from three sites on the reservoirs weekly to biweekly from October 2002 through March 2003, and once in each of April and May 2003. The field collection, laboratory analysis, and data processing procedures for this

study are described earlier (Bowles, Chapter 2, this volume). All analyses herein were conducted using the mean phytoplankton abundance (biovolume) from 3m depth at three sites. In addition, I used a phytoplankton dataset I collected on one date in each of June and August of 2001 to evaluate the effect of immigration and dispersal on community dynamics in the Highland Lake reservoir chain. The summer samples were collected from one site at the surface near the dam of all five reservoirs in the Highland Lakes (Buchanan, Inks, LBJ, Marble Falls, and Travis). Collection and processing methods are similar to Bowles (Chapter 2, this volume), except that individuals of five genera (*Navicula*, *Nitzschia*, *Scenedesmus*, *Pediastrum*, and *Anabaena*) were not separated by morphologically-distinct forms (species).

I used canonical correspondence analysis (CCA; Makarenkov and Legendre, 2002) to identify relevant ecological parameters to phytoplankton species abundance patterns across samples in each reservoir during the winter destratified period from November 2002 to February 2003 in Travis and to March 2003 in Buchanan. Species that were rare during that period were excluded from the analysis. The environmental parameters included in the matrix were water column temperature gradient, soluble reactive phosphorus, light extinction coefficient, water temperature at 3m depth, number of windy hours, and *Daphnia* and calanoid copepod biomass (Bowles, Chapter 2, this volume). The difference in water temperature between 3 and 21m depth in Travis and between 3 and 15m depth in Buchanan was used to determine the temperature gradient. The light extinction coefficient is a measure of the absorption and attenuation of surface light through depth by dissolved and particulate materials suspended in the water column (Wetzel, 2001) and in the winter months primarily is due to abiotic materials. The extinction coefficient was calculated from the exponential decay curve through the light profile across depth. The number of windy hours was estimated to be the number of hours over the prior seven days in which wind speeds exceeded 3.5 m s^{-1} in the direction of the fetch of the reservoir. *Daphnia* (Cladocera) and calanoid copepods were included as the primary grazers in freshwater systems (Sommer and Sommer, 2006). The software of Makarenkov and Legendre (2002) conducts CCA based on linear and polynomial

regression to account for nonlinear relationships between abundances and environmental variables, and uses permutation tests to assess the significance of the axes. In both lakes, the CCA based on linear regression produced significant axes while polynomial regression did not, so these results are based on the linear CCA.

In order to employ neutral theory as a null model for phytoplankton community dynamics in the reservoirs, I first estimated the role of internal dispersal and extrinsic immigration on species richness and relative species abundance using the intensive winter dataset from Travis and Buchanan, and the summer dataset from all five reservoirs of the Highland Lakes. When dispersal is limited, neutral theory predicts that species similarity among local communities is a function of distance (Chase et al., 2005). Therefore, I compared similarity indices among the summer assemblages in the reservoirs to determine if relative similarity is higher between adjacent reservoirs. I calculated the Sorenson index on presence/absence data (Legendre and Legendre, 1998) and Chao's abundance-based Sorenson index (Chao et al., 2000) using EstimateS version 7.5 (R.K. Colwell). The index of Chao includes a shared species estimator, where the number of rare shared species is used to estimate the number of unobserved shared species (Magurran, 2004). I correlated relative proximity between reservoirs to the mean similarity for both indices using Spearman rank correlation analysis on Systat 10. Richness and similarity may have been minimally underestimated due to the species that were combined into genera (see methods above).

I also estimated the effect of spatial heterogeneity on species richness in the winter assemblages by distinguishing between rare species that were "somewhere dominant" (common or dominant elsewhere over time and space in the reservoirs; Murray et al., 1999), versus those that were rare in all samples collected in the reservoirs in the summer and winter.

When immigration (M) = 0, neutral theory predicts that change in species abundance through time is a result of random processes rather than functional differences between species, where the probability of species replacement is based on relative species abundance within the local community (ecological drift; Hubbell, 2001). While

Hubbell's prediction concerned communities saturated with individuals, where species replacement occurs after mortality due to disturbance, the assumption of functional equivalence between species can be tested on any community in which changes in abundance through time are a function of population growth and mortality (also predicted to be random). Specifically, under ecological drift, the neutral theory predicts that the proportion of the total abundance contributed by any species in a local community at time t+1 is simply a function of its proportion at time t. In order to estimate the predicted species abundance patterns under the neutral theory, I used bootstrap resampling to draw 500 random samples from the community at time t to obtain a mean and 99% confidence interval for the predicted proportion of biovolume contributed by a species at time t+1. When $M > 0$, change in species abundance in the local community also will be influenced by the relative species abundance in the source area (Hubbell, 2001).

RESULTS

Richness and similarity among the phytoplankton communities

The summer mean Sorensons and Chao similarity indices were unrelated to reservoir proximity (Figure 3.1), indicating that adjacent reservoir pairs did not have greater phytoplankton community similarity relative to pairs separated by one or more reservoirs. In addition, cumulative species richness in the summer across the five reservoirs showed a similar pattern both months (Figure 3.2), increasing by only three in June and two in August downstream of LBJ.

Species richness during the winter months was consistently higher in Buchanan than Travis (Bowles, Chapter 2, this volume). Of the species collected in both reservoirs during the winter, a total of 22 were always rare, i.e., never made up more than 2.5% of the total biovolume in any sample in either reservoir. However, nine of the species were collected at abundances higher than 2.5% during the summer in Travis, Buchanan or one of the other reservoirs (data not shown). Therefore, only 13 taxa of 67 identified in samples during the winter were not found in any appreciable abundance elsewhere over space or time in the reservoirs. More extensive sampling efforts during the summer may

reduce that number. Nevertheless, on any one date during the winter, the highest proportion of these 13 taxa was 24% (8 of 33 total species detected in the sample).

Canonical correspondence analysis

In Travis, the first and second CCA axes accounted for 79.7% of the variation of the data matrix (P = 0.007 after 999 permutations; Figure 3.3) and the first six axes accounted for 99.1% of the variation. The two axes distinguished the species present early in the destratified period when the water column was homogeneous, and SRP concentrations, 3m water temperature, and light extinction were high, from those that appeared later when the water column began to stabilize and water temperature was lower. In particular, the vectors for water column temperature gradient and SRP concentration were exactly opposite, indicating a negative covariance between the two variables. Zooplankton biomass and the number of windy hours had little influence on species abundance patterns in Travis.

In Buchanan, the first and second CCA axes accounted for 83.6% of the variation of the data matrix (P = 0.031 after 999 permutations, Figure 3.4) and the first six axes accounted for 99.3% of the variation. The biplot of vectors for water column temperature gradient, SRP concentration, water temperature and the extinction coefficient was similar to that of Travis and those variables were likewise important to species abundance patterns. However, in Buchanan, calanoid copepod biomass and the number of windy hours had higher loadings on the first two axes relative to Travis, indicating greater influence of those variables on species abundance in Buchanan.

Species-gradient relationships

In Travis, the water column temperature gradient distinguished diatom species from flagellates (Figure 3.5). Two cryptomonad flagellate species, *Cryptomonas phaseolus* and *Campylomonas rostratiformis*, dominated the winter phytoplankton community (Figure 3.6), but showed different responses to the temperature gradient. *Cryptomonas phaseolus* comprised more of the total biovolume when the water column was homogenous and *C. rostratiformis* increased as the temperature differentiation began to occur across depth (Figure 3.6). Conversely, the contribution of *C. phaseolus* to total

biovolume decreased under slight water column stability when SRP concentrations dropped (Figure 3.6).

The maximum abundance of two large diatom species, *Aulacoseira granulata* and *Melosira varians*, occurred early in the destratified period in Travis (Figure 3.7). However, the two showed slightly different patterns in response to water column temperature gradient and the light extinction coefficient, where *M. varians* was relatively more dominant when the water column was homogenous and the extinction coefficient was high (Figure 3.7).

In Buchanan, the maximum abundance of diatoms and flagellates were not distinguished strongly by the temperature gradient because species within each group showed different abundance patterns, likely due to erratic stability and the influence of wind (Bowles, Chapter 2, this volume). For example, the relative abundance maximum of *A. granulata* was separated by time compared to other large diatom species, *Aulacoseira* cf. *distans* and *Stephanodiscus agassizensis* (Figure 3.8). The latter two species showed similar but slightly distinct abundance patterns. The proportion of total biovolume for both species increased in response to a high number of windy hours over the prior seven days, but the two species showed different sensitivity to water column temperature gradient across depth (Figure 3.8).

Contrary to Travis, *C. rostratiformis* dominated the phytoplankton community over the winter destratified period (Figure 3.9). While *C. phaseolus* comprised a higher proportion of the total biovolume when the water column was homogenous, *C. rostratiformis* was little affected by water column temperature gradient (Figure 3.9). However, *C. rostratiformis* decreased in abundance relative to *C. phaseolus* on two dates in which calanoid copepod biomass was high (Figure 3.9).

Neutral dynamics

With few exceptions, the proportional abundance of the diatom and flagellate species were well outside of the 99% confidence interval predicted by the neutral theory assuming M=0 (Figure 3.10 and 3.11). The exceptions occurred when the abundance of a species was 0 (below detection), such as for *C. rostratiformis* in November in Travis

(Figure 3.10) and *Aulacoseira* cf. *distans* in November in Buchanan (Figure 3.11), or when the contribution of a species to total biovolume was similar for two consecutive sampling dates.

DISCUSSION

Immigration, dispersal, and the metacommunity framework

Immigration from regional species pools to local communities can be a relevant factor in species abundance patterns (Mouquet and Loreau, 2003). Neutral theory (Hubbell, 2001) and other metacommunity theories (reviewed in Holyoak et al., 2005) make specific predictions about the relationship between spatial heterogeneity and immigration in structuring the local community. In this study, I explored species richness and similarity patterns across a highly connected system of five reservoirs to evaluate the role of extrinsic immigration and internal dispersal on the phytoplankton communities.

1. Cumulative richness showed a minimal increase downstream of the third reservoir during the summer. This indicates that immigration from outside the system had negligible influence on the summer assemblages, as nearly all taxa collected in Marble Falls and Travis can be accounted for by dispersal from upstream (there is no reason to believe that immigration from outside the system would be lower in these two reservoirs). Since many phytoplankton species are passive, and even flagellated forms cannot traverse long distances, the primary mode of internal dispersal is hydrological.
2. The species richness in Travis was lower than Buchanan over most sample dates. It is highly doubtful that this is due to a dispersal barrier between Marble Falls and Travis, and may instead reflect the productivity/richness relationship (Dodson et al., 2000).
3. The majority of species on all dates during the winter were "somewhere-dominant" (Murray et al., 1999). This suggests that spatial and temporal heterogeneity are the primary drivers of richness in this system, as suggested by Smith et al. (2005). Many algal species have an inactive or resting stage that

allow them to persist in the local community until conditions are favorable for growth (and it is possible that species without this mechanism can be maintained in a lake at an undetectable abundance).

4. Similarity among the reservoir phytoplankton communities was unrelated to proximity.

These findings provide strong support for species sorting (Holyoak et al., 2005) as the primary mechanism structuring the phytoplankton communities in the reservoirs, where dispersal functions to distribute species across habitats, but local community structure is driven by environmental parameters. Species sorting predicts that an increase in a local population of a species primarily is due to growth in response to environmental factors (consistent with its niche) rather than immigration. Cottenie (2005) also found that freshwater plankton (as passive dispersers) tracked environmental parameters with little influence of spatial dynamics, consistent with species sorting.

In addition, the inflow to the reservoirs replaces no more than 3% of the total volume of the reservoirs over a 7-day period (Lower Colorado River Authority, unpublished data) not including large spates, which did not occur during the sampling period for this study. Therefore dispersal within the system contributes no more than a minimal amount to the change in abundance between two time periods.

Niche differences among species along environmental gradients

The distinction between diatoms and flagellates along the gradient of water column stability in Travis is similar to the framework of Reynolds (1995) that distinguishes "ruderal" species (those associated with deep circulation or continuous mixing), from small, fast-growing "invasive" species that tend to increase with the onset of stratification. Perhaps the most surprising result is that the transition from diatoms to flagellates occurred under extremely small temperature gradients, specifically when the water temperature at 3m and 21m depths differed by less than 0.2ºC. The depth profile of flagellates followed that of the temperature profile on most dates in both reservoirs, i.e., when the water temperature gradient increased across depth, the abundance of flagellates

at 3m increased relative to the abundance at 21m (Bowles, Chapter 2, this volume). This indicates that the temperature gradient was a good indicator of mixing intensity.

Relative abundance of species within the two groups, however, could be distinguished along environmental gradients. In Travis, the larger cryptomonad species, *Campylomonas rostratiformis*, was more susceptible to a homogenous water column than *Cryptomonas phaseolus* presumably due to low light levels from deep mixing. This is consistent with culture data (Gervais, 1997) where *C. phaseolus* had a higher growth rate at low light levels than *C. rostratiformis*. In addition, the response to dissolved phosphorus depletion may be different between the two species, as the contribution of *C. phaseolus* to total biovolume dropped at higher water column stability but lower SRP levels. Indeed, the location of *C. phaseolus* is very near the SRP vector in the CCA biplots of both reservoirs, indicating the species was associated with relatively high SRP concentrations. In Buchanan, *C. rostratiformis* was more abundant relative to *C. phaseolus* through the entire destratified period, likely aided by frequent water column stability. When mixing did occur it was short-lived and shallow relative to Travis. However, *C. rostratiformis* appeared to be susceptible to grazing by calanoid copepods, whereas *C. phaseolus* was less so. Indeed, copepods are selective grazers with a preference for larger cells (Sommer and Sommer, 2006), indicating that cell size contributed to the relative difference in abundance of these two species when calanoid copepod biomass was high.

Similarly, the relative relationships among large diatom species differed in response to water column stability, light extinction, and windiness in the reservoirs. Diatoms are known to tolerate low light levels and require water column mixing to avoid sinking (Diehl, 2002). However, sinking rates are related to cell density and cell size (Smayda, 1970). *Melosira varians* is larger than *Aulacoseira granulata* and may require greater mixing intensity to maintain net growth in the water column. This is consistent with the abundance patterns in Travis, where the contribution of *M. varians* to total biovolume dropped relative to that of *A. granulata* when the water temperature gradient exceeded 0.03ºC. In Buchanan, the large diatom species *Stephanodiscus agassizensis*

and *Aulacoseira cf. distans*, responded well to windiness, likely due to an increase in wind-induced mixing. However, the species differed in relative abundance in response to temperature differentiation across depth. The former may be more tolerant of low light levels associated with deep mixing than the latter. Unfortunately, no empirical data are available on relative light requirements among the diatom species found in these reservoirs.

Neutral theory

Species abundance distributions in tropical forest communities are consistent with the predictions of neutral theory (Hubbell, 2001, 2005), which posits that species are functionally equivalent at the local scale, and that differences in their relative abundance can be attributed to dispersal and recruitment limitation and to stochastic growth and mortality. However, dispersal limitation cannot explain temporal and spatial differences in phytoplankton communities of Travis and Buchanan since dispersal from outside the system seems to have little influence on the phytoplankton communities on an annual time scale and internal dispersal can affect no more than 3% of the change phytoplankton abundance over a seven-day period. Further, the canonical correspondence analyses, which included only environmental variables, explained 99% of the variation of the matrix in both reservoirs. This is strong supporting evidence that dispersal was minimally important to species abundance patterns because variables describing space or inflow rate were not necessary in the analysis, but more importantly, that ecological factors were the overwhelming driving force for the abundance patterns.

Finally, this study demonstrates for the first time that the abundance of phytoplankton species along environmental gradients are not consistent with neutral theory. The change in abundance of several species over time was consistently and significantly outside of the trajectory expected under ecological drift. Indeed, the abundance distribution in grasses (Harpole and Tilman, 2006) and of corals in reefs (Dornelas et al., 2006) showed a significant departure from the zero-sum multinomial distribution, another prediction of neutral theory (Hubbell, 2001).

In summary, these phytoplankton communities exhibited non-neutral relationships to environmental variables during mixing, consistent with apparent niche differences among species and likely due to differences in cell morphology or physiology. In addition, soluble reactive phosphorus concentration was among the parameters most relevant to species abundance in both reservoirs, indicating that competitive processes cannot be ignored during mixing. While SRP concentration negatively co-varied with water column stability, and many species likely were responding to the latter, the proportional abundance of at least one species was depressed when SRP concentration dropped. This study supports theoretical work that demonstrates niche trade-offs are an important precursor to coexistence between species even under harsh conditions (Chesson, 2000), and can include tolerance to stressful conditions as well as competitive ability (Chase and Leibold, 2003).

Figure 3.1. Correlations between reservoir proximity and the Sorensen similarity index (A), and Chao's abundance-based Sorenson index (B) across five reservoirs of the Highland Lakes, Texas. Similarity index values are the means calculated from samples collected in June and August of 2001 at the surface near the dam in each reservoir. A reservoir proximity value of zero indicates adjacent reservoirs, while the remaining values indicate the number of interceding reservoirs.

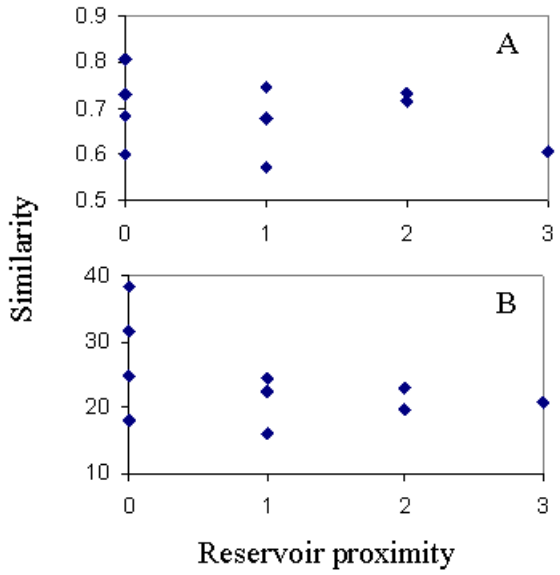


Figure 3.2. Species richness (bars) and cumulative species richness (points) of samples collected from five reservoirs of the Highland Lakes, Texas in June and August of 2001. Samples were collected from the surface near the dam in each reservoir. Reservoirs are in order of occurrence upstream to downstream.

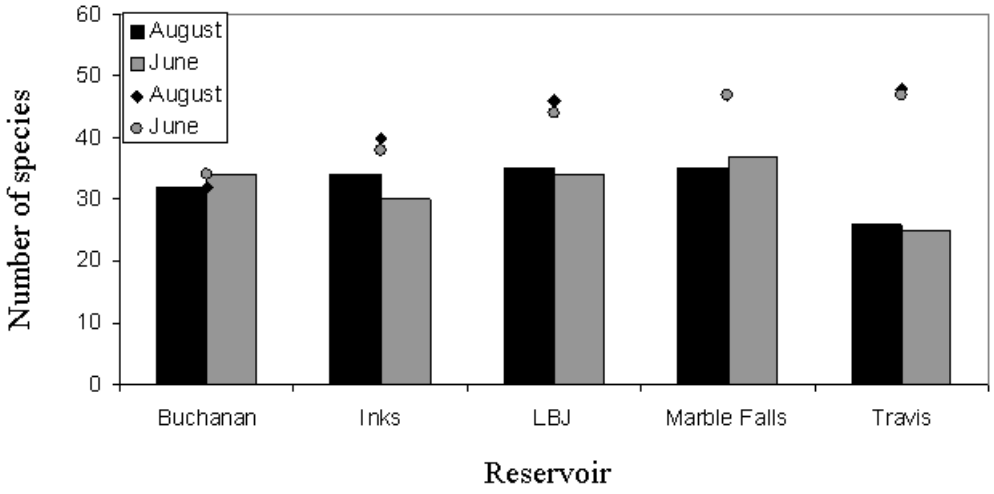


Figure 3.3. Canonical correspondence analysis ordination biplot of phytoplankton species abundance and environmental variables from Travis reservoir. Data were collected on a weekly or biweekly basis during the winter destratified period from November 2002 through February 2003. Species are represented by points and environmental variables by arrows. One arrow represents *Daphnia* and calanoid copepods. Species abundance is the mean of samples collected at 3m depth at three sites on the reservoir. T_3-T_{21} = difference in water temperature between 3m and 21m depth, MV = *Melosira varians*, AG = *Aulacoseira granulata*, CR = *Campylomonas rostratiformis*, CP = *Cryptomonas phaseolus*.

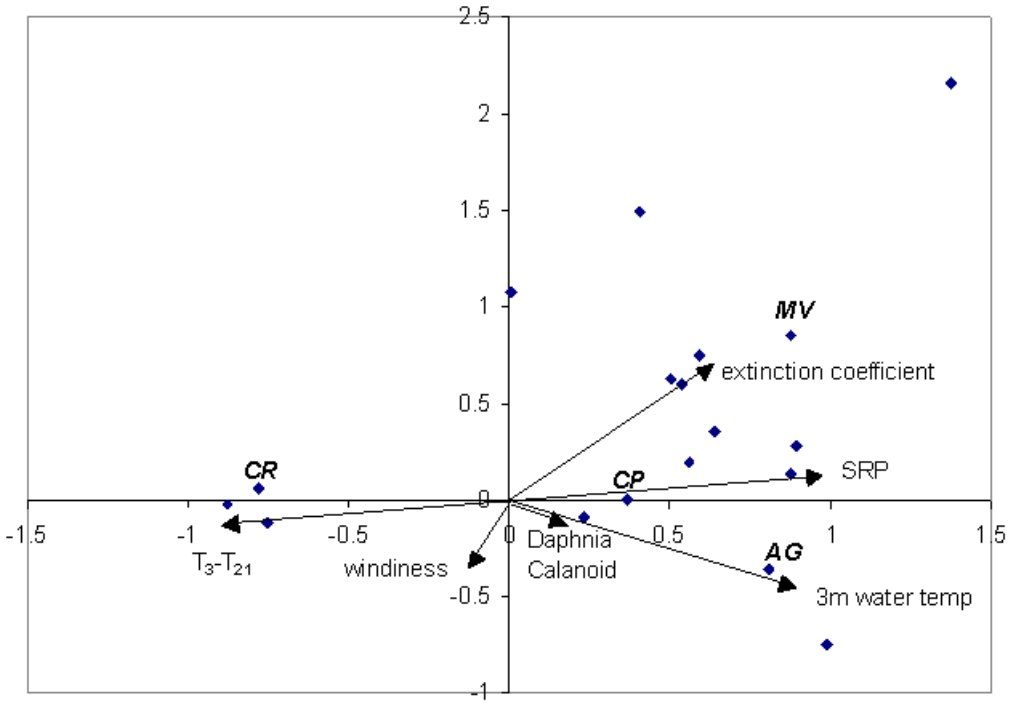


Figure 3.4. Canonical correspondence analysis ordination biplot of phytoplankton species abundance and environmental variables from Buchanan reservoir. Data were collected on a weekly or biweekly basis during the winter destratified period from November 2002 through March 2003. Species are represented by points and environmental variables by arrows. The biplot position of *Daphnia* is at the origin. Species abundance is the mean of samples collected at 3m depth at three sites on the reservoir. T_3-T_{21} = difference in water temperature between 3m and 21m depth, AD = *Aulacoseira* cf. *distans*, AG = *Aulacoseira granulata*, SA = *Stephanodiscus agassizensis*, CR = *Campylomonas rostratiformis*, CP = *Cryptomonas phaseolus*.

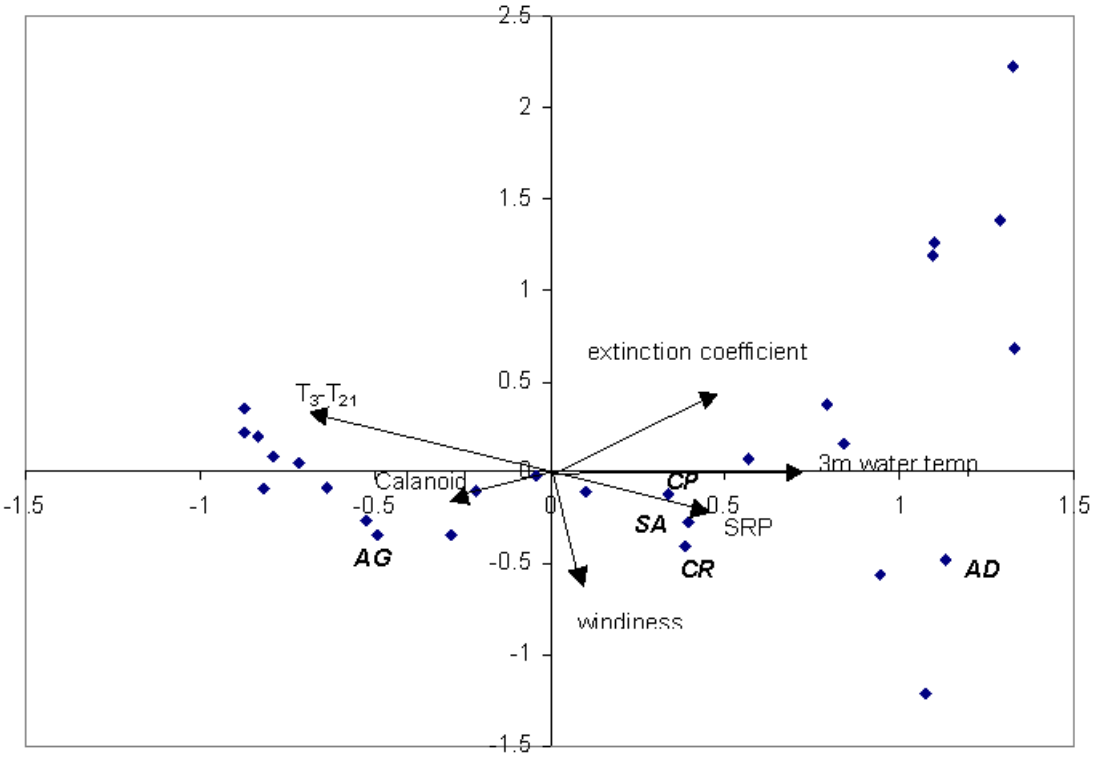


Figure 3.5. Total biovolume contributed by diatoms and flagellates versus water temperature gradient across depth in Travis reservoir during the winter destratified period from November 2002 through February 2003. Total biovolume is the mean of samples collected at 3m depth at three sites on the reservoir. Temperature gradient is the log of the difference in water temperature between 3m and 21m depth in degrees C.

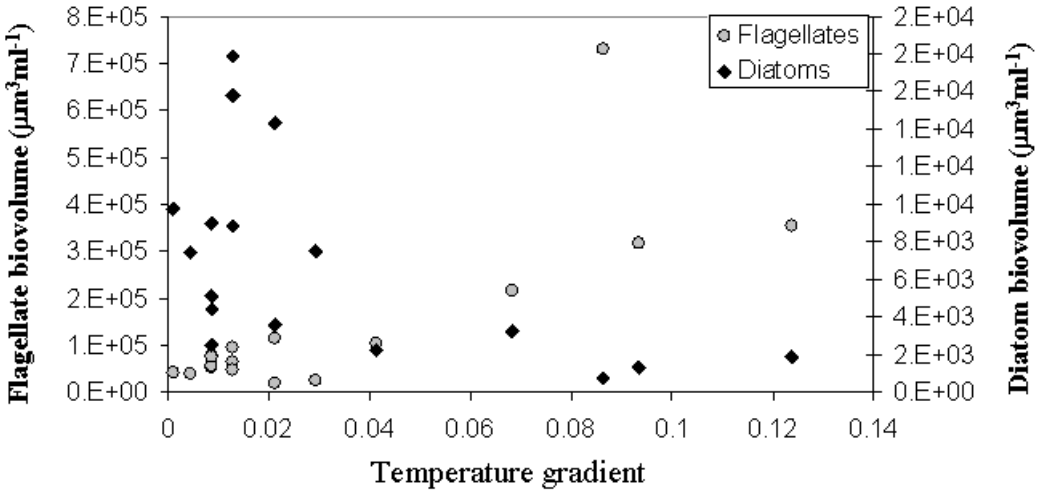


Figure 3.6. (A) Proportion of total biovolume contributed by *Campylomonas rostratiformis* and *Cryptomonas phaseolus* over time. (B) Relative contribution to total biovolume (bubbles) of *C. rostratiformis* and *C. phaseolus* versus the water temperature gradient and soluble reactive phosphorus (SRP) concentration. Data were collected during the winter destratified period in Travis. Temperature gradient is the log of the difference in water temperature between 3m and 21m depth in degrees C. Contribution to total biovolume is the mean of samples collected at 3m depth at three sites on the reservoir. Bubbles in (B) are sized relative to the largest value.

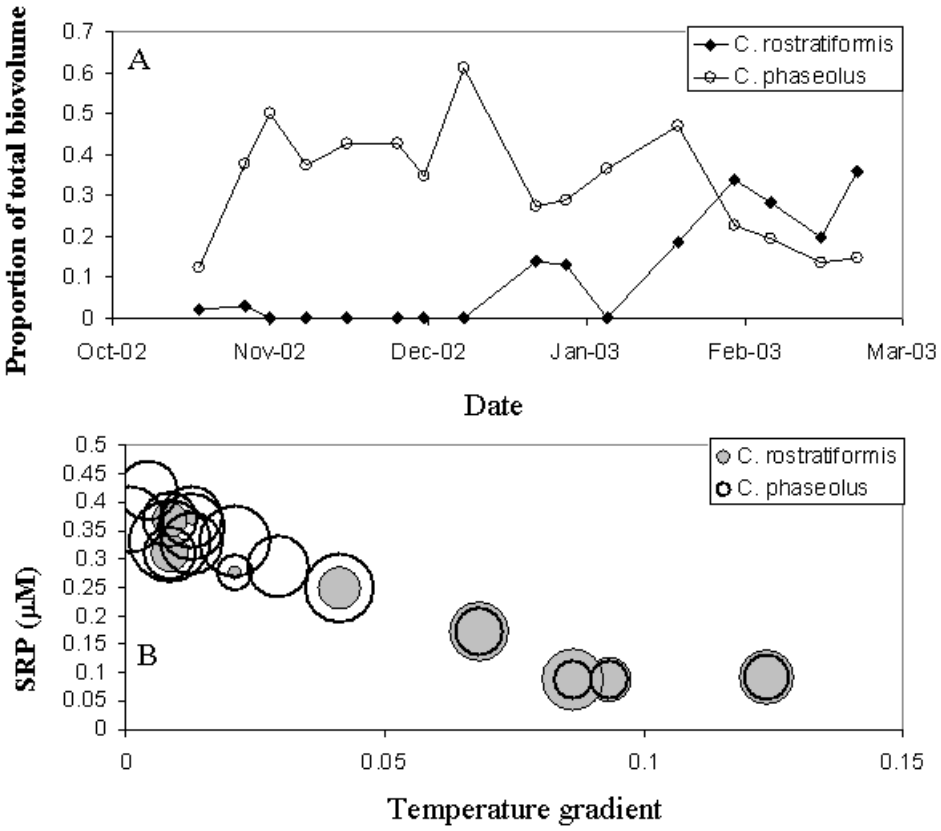


Figure 3.7. (A) Proportion of total biovolume contributed by *Aulacoseira granulata* and *Melosira varians* over time. (B) Relative contribution to total biovolume (bubbles) of *A. granulata* and *M. varians* versus the water temperature gradient and water extinction coefficient. Data were collected during the winter destratified period in Travis. Temperature gradient is the log of the difference in water temperature between 3m and 21m depth in degrees C. Contribution to total biovolume is the mean of samples collected at 3m depth at three sites on the reservoir. Bubbles in (B) are sized relative to the largest value.

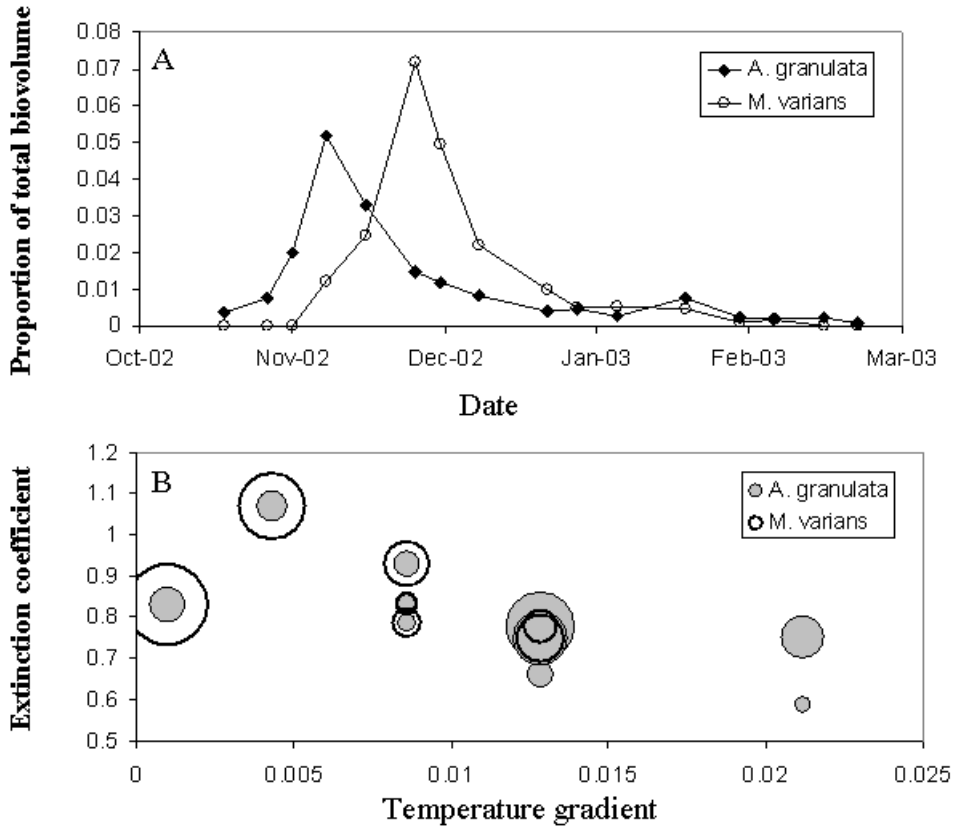


Figure 3.8. (A) Proportion of total biovolume contributed by *Aulacoseira granulata*, *Stephanodiscus agassizensis* and *Aulacoseira* cf. *distans* over time. (B) Relative contribution to total biovolume (bubbles) of *S. agassizensis* and *A.* cf. *distans* versus the water temperature gradient and windiness. Data were collected during the winter destratified period in Buchanan. Temperature gradient is the log of the difference in water temperature between 3m and 21m depth in degrees C. Windiness is the number of hours over the prior seven days in which wind speeds exceeded 3.5 m s^{-1} in the direction of the fetch of the reservoir. Contribution to total biovolume is the mean of samples collected at 3m depth at three sites on the reservoir. Bubbles in (B) are sized relative to the largest value.

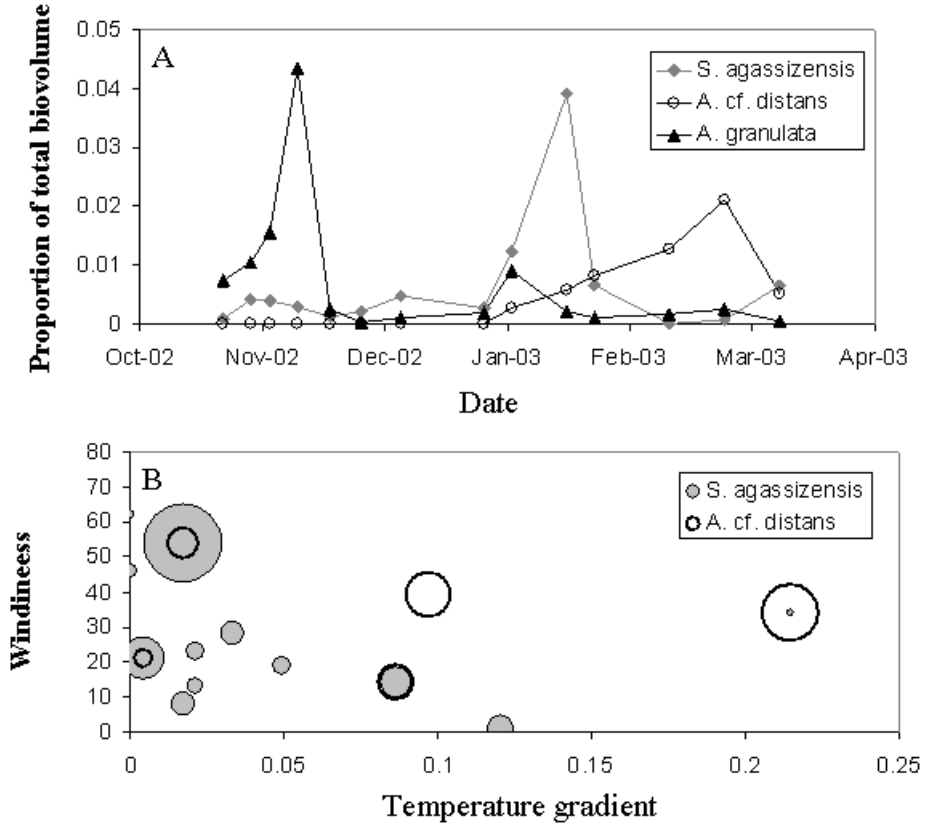


Figure 3.9. (A) Proportion of total biovolume contributed by *Campylomonas rostratiformis* and *Cryptomonas phaseolus* over time. (B) Relative contribution to total biovolume (bubbles) of *C. rostratiformis* and *C. phaseolus* versus the water temperature gradient and calanoid copepod biomass. Data were collected during the winter destratified period in Buchanan. Temperature gradient is the log of the difference in water temperature between 3m and 21m depth in degrees C. Contribution to total biovolume is the mean of samples collected at 3m depth at three sites on the reservoir. Bubbles in (B) are sized relative to the largest value.

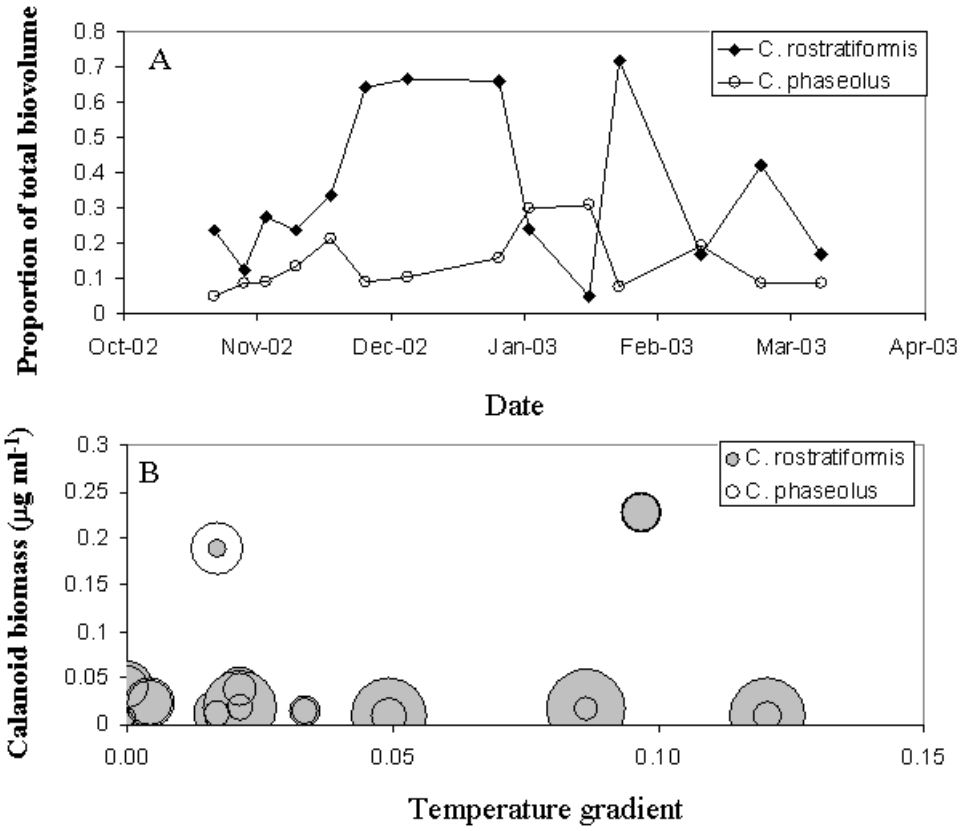


Figure 3.10. Departure of the observed proportional abundance of *Campylomonas rostratiformis* and *Cryptomonas phaseolus* (A) and *Melosira varians* and *Aulacoseira granulata* (B) from the predicted proportional abundance under the neutral theory. The gray shading represents the bootstrapped 99% confidence interval around the mean predicted by the neutral theory (not apparent in A). Only the larger confidence interval of the two species is shown. Data were collected during the winter destratified period in Travis reservoir from November 2002 through February 2003. Contribution to total biovolume for each species is the mean of samples collected at 3m depth at three sites on the reservoir.

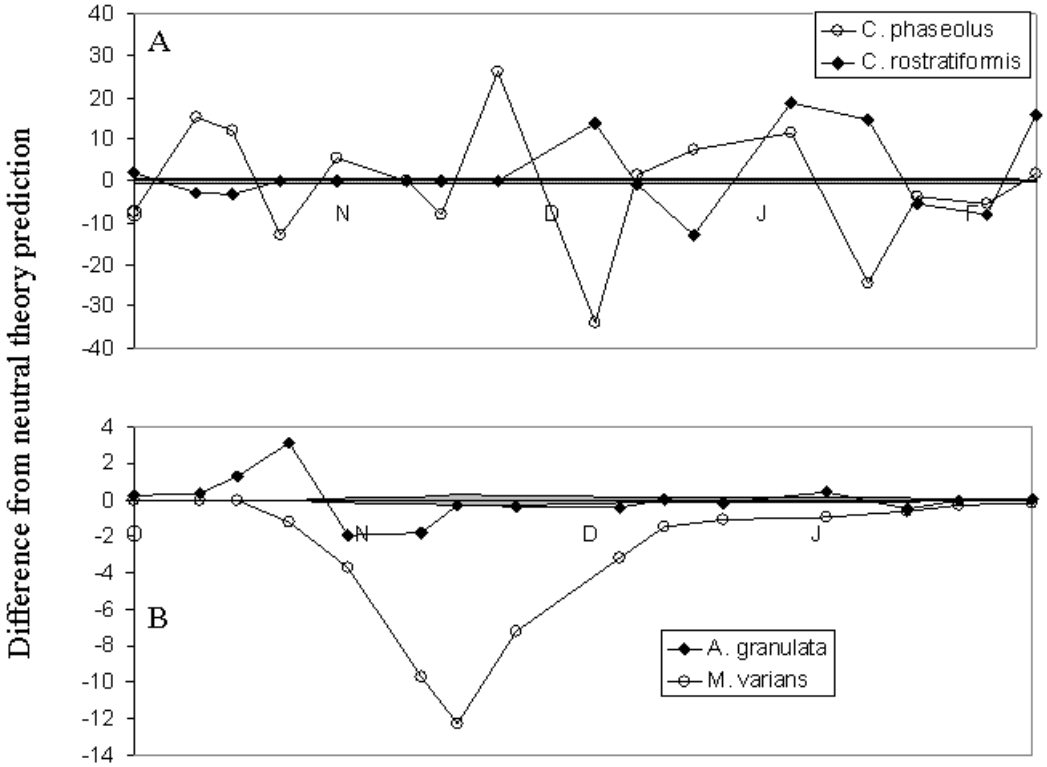
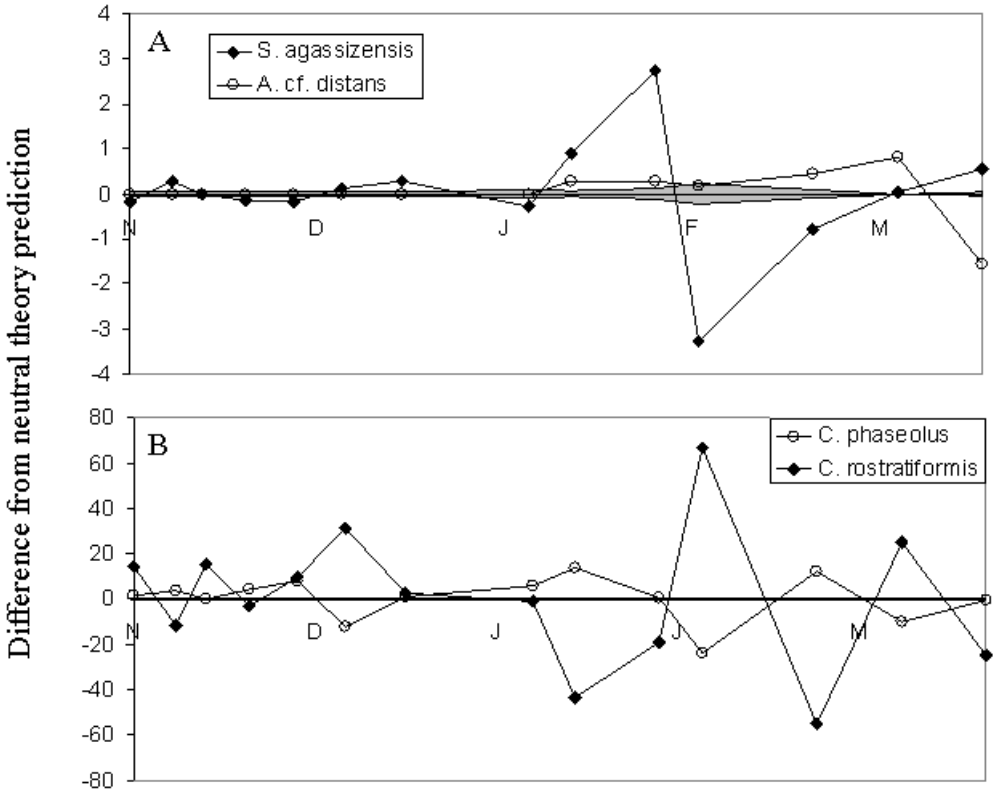


Figure 3.11. Departure of the observed proportional abundance of *Stephanodiscus agassizensis* and *Aulacoseira* cf. *distans* (A) and *Campylomonas rostratiformis* and *Cryptomonas phaseolus* (B) from the predicted proportional abundance under the neutral theory. The gray shading represents the bootstrapped 99% confidence interval around the mean predicted by the neutral theory (not apparent in B). Only the larger confidence interval of the two species is shown. Data were collected during the winter destratified period in Travis reservoir from November 2002 through March 2003. Contribution to total biovolume for each species is the mean of samples collected at 3m depth at three sites on the reservoir.



CHAPTER 4. Effect of local sampling scale on perceptions of phytoplankton species maxima and co-occurrence

INTRODUCTION

Scale of observation is of paramount concern in ecological study design (Wiens, 1989; Levin, 1992) and can have dramatic effects on the perception of ecological relationships (Willis and Whittaker, 2002), diversity (Willig et al., 2003), similarity between communities (MacNally et al., 2004) and interpretation of field experiments (Frost et al., 1988). For instance, the subdivision of species into groups according to functional traits (Wilson, 1999) is scale-dependent because the assignment of group boundaries is an arbitrary designation (Hooper et al., 2005; Levin, 1992). Non-random co-occurrence of species has been used as a basis for identifying coexistence (Naselli-Flores et al., 2003). However, while coexistence has been narrowly defined (Chesson, 2000), identification of co-occurrence is scale-dependent and simply may be an artifact of the limits of our understanding of the distribution of the organisms.

Phytoplankton associations are variously defined, but generally are identified by non-random co-occurrence of phytoplankton species, and are proposed to represent similar species response to properties of the environment (Reynolds, 1984; Legendre, 1973). Such associations have been explored across lakes (Reynolds, 1984; Earle et al., 1987; Hutchinson, 1967), oceanic habitats (Venrick, 1971; Legendre, 1973), and season (Reynolds, 1984; Legendre, 1973), and are useful for broad interpretations of environmental characteristics and species autecology. Reynolds (1980, 1984, 2000) defined associations to be 'assemblages of species that share closely similar phasing of increase, relative abundance and decrease' identified by 'reproducible, non-random, co-occurrence' and derived associations through a qualitative grouping of samples by dominant and subdominant species. Others have used a probabilistic similarity index (Legendre, 1973), Fager recurrent group analysis (Fager, 1957; Venrick, 1971) or ordination (Earle et al., 1987).

Recommendations for the appropriate sampling intensity relevant to ecological processes of lentic phytoplankton, including grain size (sample volume) and spatial and

temporal extent (Addicott, 1987; MacNally and Quinn, 1998), are rare, but would be extremely useful. For instance, generation time for phytoplankton can be as short as 0.5 d^{-1} (Reynolds, 1993), suggesting that collections should occur more frequently than weekly to evaluate population dynamics for some species. An understanding of the spatial pattern of a variable, such as phytoplankton abundance or primary productivity (Carney et al., 1988; PinelAlloul et al., 1996; Walsby, 1997), is an important prerequisite to field studies, whether it is incorporated as a characteristic of interest or removed through study design (Dutilleul, 1993).

My purpose was to investigate the extent that local sampling scale affects the perception of species abundance maxima across time and space in a lake and creates the impression of association between species. I use the high-resolution phytoplankton dataset of Interlandi et al. (1999) from three lakes of the Greater Yellowstone Ecosystem (GYE), in which they found that abundance maxima of species rarely co-occurred over space and time. First, I examined the effect of spatial and temporal sampling intensity on the identification of the location of abundance maxima and on the perception of association between two species across all GYE lakes. For this analysis I concentrated on two diatom species, *Asterionella formosa* (AF) and *Aulacoseira subarctica* (AS), which have been classified by Reynolds et al., (2002) as a recurrent association (functional group) in soft-water lakes attributed to a mutual reliance on turbulence for suspension. Both species occur in all three GYE lakes. In addition, I compare three measures of association between species drawing from the concepts of 'co-occurrence', 'similar increase and decrease' and 'mutual abundance' cited above, to determine if the identification of significant co-occurrence between species is dependent on analysis method.

METHODS

Data collection

The data used in this study were collected from Yellowstone and Lewis Lakes in Yellowstone National Park and Jackson Lake in Grand Teton National Park in 1996 and

1997 (Interlandi et al., 1999). Lake descriptions, and data collection and analysis methods are presented in Interlandi et al., (1999). Briefly, samples for phytoplankton counts were collected approximately weekly from Yellowstone and Jackson Lakes and every 10 days from Lewis Lake from ice-out to mid-October at one site in each lake, and were taken at 5-m intervals from the surface to 50 m in Yellowstone Lake, to 30 m in Jackson Lake, and to 25 m in Lewis Lake. Phytoplankton samples were immediately fixed with Lugol's solution and counts were performed using the inverted-microscope technique. Abundance data are presented as total biovolume.

Sampling scale and measures of association

I artificially reduced the dataset from all lakes in both years to simulate the effect of different spatial or temporal sampling regimes on the identification of abundance maxima and co-occurrence of species. For the monthly data set, I included the first sample gathered from each lake each year, and then samples taken at approximately 30-day intervals thereafter. The biweekly data set similarly included samples taken at 14-day intervals. Reduced depth intervals included three samples at 10m intervals (surface, 10m, and 20m), surface samples only, and water column average. Water column average is the mean of the species abundance across depths for each sampling date and was used to represent depth-integrated samples (samples across depths combined into one sample). All sampling intervals were selected based on those found in the literature or recommended for lake monitoring programs.

I pinpointed the date and depth of the abundance maxima for AF and AS using the entire dataset, and in the subsets of data drawn to imitate lesser sampling regimes (described above) in the three lakes in both years. In addition, to demonstrate that the effect of sampling intensity on species abundance patterns was not restricted to those two diatoms, I also similarly evaluated species abundance maxima for all dominant species in Jackson Lake in 1997. Dominant species were defined as those that comprised at least 10% of the total biovolume on any date in the lake that year (excluding small coccoid cyanobacteria and small flagellates that could not be distinguished into species). While

the response to sampling intensity was apparent in all lakes, I chose Jackson Lake because it contained the most number of dominant species through the growing season.

I evaluated the effect of sampling intensity and analysis method on the apparent association between AF and AS. I applied three simple, non-parametric statistical tests to determine co-occurrence between the two species. All were evaluated at $p < 0.01$ because multiple comparisons were made. First, frequency tables were constructed with presence/absence data of the two species across the various sampling schemes. Fisher's exact test (Systat 10, Systat, Inc.) was used to test the degree of association because all tables contained at least one cell with a value of 5 or less (Legendre and Legendre, 1978).

Second, Spearman rank correlation (SYSTAT 10, Systat, Inc.) was used to measure the strength of the linear relationship between AF and AS abundance. Prior to the analysis, I looked for spatial and temporal autocorrelation in the data because of the proximity of the sample points in time and space. For temporal autocorrelation, I used CurveExpert 1.3 (© Daniel Hyams) to fit the time series of abundance at each depth to a linear or nonlinear regression model to obtain residuals. I then correlated the residuals with their lag 1 residuals using Pearson's correlation (Systat 10, Systat, Inc.) and found no evidence of serial autocorrelation. Spatial autocorrelation was evaluated using the Mantel test on PC-ORD (© MGM Software Design) and was found on some sampling dates across depths. Because a remedy for spatial autocorrelation is not available for small sample sizes (6 – 11 depths per sampling date), I compared the results of the naïve test (without correction for autocorrelation) to the evaluation of significance after removing 2 df for every sampling date and found no change in the assessment of significance.

Finally, I used a sign test (Conover, 1980) to investigate the similarity in the direction of change of AF and AS abundances over time (synchrony):

> Let "+" = a mutual change in abundance between two successive sampling dates (either both increase or both decrease in abundance)
> Let "-" = abundance of one species increases while the other decreases, or abundance of one species changes while the other does not

One-tailed test:
$H_0 = P(+) \leq P(-)$
$H_1 = P(+) > P(-)$

A change in abundance was considered an increase or decrease only when it exceeded a presumed counting error of 10% (Lund et al., 1958). The numbers of "+" and "-"were assessed separately for each depth each lake year, and then summed.

RESULTS

Abundance maxima of AF and AS across the GYE lakes in 1996 and 1997

The AF maximum shifted as much as 60 days or 25m in the reduced datasets (Table 4.1). This reflected the fact that the species was distributed throughout the water column in the spring, but also showed a short-lived, isolated abundance peak in deeper waters during summer stratification in Yellowstone and Jackson in 1997. The reduction in temporal sampling intensity from weekly to biweekly, even without any loss in spatial intensity, caused this later abundance peak to be missed. Likewise, the reduction of spatial sampling intensity to 3 depths without any loss of temporal intensity also missed this peak (Table 4.1). Similarly, AS was maximally abundant early in the year, but also showed a high abundance in the epilimnion or hypolimnion after stratification (Table 4.1). Both the biweekly and 30-day sampling schemes, or restriction of sample collection to the surface, identified the later surface subpeak as an overall maximum.

Abundance maxima of dominant species across Jackson Lake in 1997

Artificial reduction of the spatial and temporal resolution of the dataset resulted in considerable departures in the identification of abundance maxima for some species (Table 4.2). This is particularly true for species which persisted throughout the sampling period, but whose abundance shifted by depth through time.

Reduced spatial and temporal scale also created the illusion of coincident abundance maxima between two or more species that was not evident in the entire dataset (Table 4.2). For example, AF and AS appeared to share an abundance maximum on JD 155 at 5m depth when the temporal sampling intensity was biweekly. However, the true

abundance maximum of both species was different from this sub-peak in time and depth. Loss of spatial scale, either through collecting samples only from the surface or through integrating samples across depth, produced the appearance of many coincident peaks among the dominant species (Table 4.2). Most notably, the abundance peaks of SM, AF, and AS coincide early in spring mixing when the samples across depth were combined. This is because deeper samples with high abundance of AF and AS were diluted by samples with relatively lower abundance at the surface, particularly in the case of AF after stratification. Conversely, in the case of *Eudorina* sp. and *Dinobryon* sp., mutual abundance peaks were detected on JD 239 at 5m depth when the entire dataset was examined. However, reduction in spatial sampling intensity, or temporal intensity to monthly, resulted in the divergence of their abundance maxima.

Not every species reacted in the same way. For instance, the *Stephanodiscus minutulus* (SM) abundance maximum is always on JD 141 regardless of sampling scale (Table 4.2). This is because SM was extremely seasonal in abundance, demonstrating a high abundance during spring mixing but essentially absent from samples after stratification. Maxima of *Cyclotella bodanica* (CB), *Eudorina* sp., *Dinobryon* sp., *Dactylococcopsis* sp. and *Aulacoseira* sp. did not shift more than 20 days in any sampling regime because they also had a relatively brief appearance in the phytoplankton. Underscoring this, *Dactylococcopsis* sp., which has a brief but strong spike in abundance (44% of the total biovolume of phytoplankton on JD 206) was entirely missed in the monthly sampling regime.

Association between AF and AS

The frequency table analysis using presence/absence data across all sampling scales was significant because most samples contained a detectable number of AF and AS (Table 4.3). However, I repeated the analysis on the entire dataset using the median as the point of division (results not shown). This analysis was not significant, indicating that the co-occurrence of mutually low or high abundance of the two species was not greater than would be expected by random chance.

In most instances, the extent of correlation in abundance of the two species changed as a result of sampling structure (Table 4.3). The strength of the correlation over the entire dataset was driven to a large extent by the near 1:1 relationship across depth during the period between JD 142 and JD 170 (22 May to 19 June) in Yellowstone Lake in 1997 (Figure 4.1). This explains the drop in correlation when this time period was excluded and the higher positive correlation between the two species before stratification. However, when the data were reduced to a window during late spring before stratification (JD 162-191), the correlation became significantly negative. During this period toward the end of spring mixing and the beginning of stratification AF increased in abundance while AS decreased. Further, restricting the samples to the surface increased the correlation between the two species, particularly when the sampling frequency was reduced to bi-weekly. As noted for Jackson Lake in 1997 both species were abundant after stratification, and in all lakes AS showed a high abundance at the metalimnion. Surface sampling, therefore, created the appearance of mutual high abundance during spring mixing and mutual low abundance after stratification. This is consistent with the results of the Jackson Lake analysis shown above. Integrating abundance over the entire water column did not increase the correlation between AF and AS. This can be attributed to the fact that high average abundance of the two species over the entire water column did not occur on the same dates.

In no case did I find synchrony between the two species using the sign test (Table 4.3), indicating that the number of sample intervals in which the two species exhibited a mutual change in abundance did not tend to be greater than the number of intervals that they did not, and sampling intensity had no effect on this.

Sampling extent and interval

The distribution of species maxima across space and time in the lakes (Figure 4.2) demonstrates that samples collected below the epilimnion have a lower probability of capturing a species maximum, although two species were maximally abundant there. However, the number of species maxima does not change over time, indicating that

samples collected early in the year are not less likely to contain a species abundance maximum.

Species with abundance maxima prior to stratification were concentrated in the upper depths, indicating that slight water column stability may have been adequate to increase populations in areas of light penetration (Bowles, Chapter 2, this volume). However, the distribution of species during mixing extended the entire water column and the abundance of dominant species exceeded 10% of the total biovolume in all sample collected across depth prior to stratification.

Sampling effort has a predictable effect on the number of species detected. The number of dominant species captured linearly decreases with increasing sampling interval (Figure 4.3). In addition, reduced temporal sampling frequency also increased the appearance of co-occurrence between dominant species (Figure 4.4). On several occasions, the abundance maximum was not collected and a sub-maximum was identified as the maximum. Nevertheless, the loss of temporal sampling intensity increased the frequency of joint maxima after about the 30-day interval. Decreasing the sampling intensity across depth had little effect on apparent co-occurrence (Figure 4.5), except when only one sample was collected.

DISCUSSION

Species maxima and co-occurrence

Interlandi et al. (1999) demonstrated that phytoplankton species maxima in the GYE lakes rarely coincided spatially and/or temporally. Because space and time in lakes also represents a clear separation of broad ecological factors such as temperature, nutrients and light, it is not surprising that differences in their ecologies (Interlandi et al., 1999) translated into distinct spatial and temporal abundance maxima of species. Given this, there is a risk of changing the perception of their spatial distribution, and also of relevant ecological relationships, by changing the sampling scale. For instance, while AS was present, and even at times maximally abundant, in the spring, the species could be found at relatively high abundance below the thermocline after stratification in all three

lakes (Interlandi et al., 1999). This is attributable to deep light penetration that allowed the species to take advantage of high nutrient levels because of minimal light requirements (Interlandi et al., 1999). A restriction of sampling to the epilimnion would have missed important data relevant to the ecology of AS. The tendency of flagellates across several taxonomic groups to align themselves into bands along light gradients in the water column in stratified conditions (Clegg et al., 2003; Sommer, 1982; Olli and Seppala, 2001) supports the argument that an understanding of vertical patterns certainly is important for ecological investigations of phytoplankton communities. Similarly, short generation times for algae (Reynolds, 1993) underscore the importance of temporal scale in phytoplankton studies. Indeed, in this study, temporal and spatial reductions of sampling intensity changed the appearance of abundance maxima over time and space for several species. In the case of AF, its highest abundance levels were detected during spring mixing in all reduced sample schemes, while the true peak in abundance occurred in deeper waters after stratification. This may have implications for the assumption that the species requires circulation to remain in the water column (Reynolds et al., 2002).

The results of this investigation also indicate that sampling scale can create the impression of mutual abundance maxima across species in a community. This could mislead one to the conclusion that two (or a group of) species possess more ecological similarity than actually exists and emphasizes the need for caution when grouping species into associations based on co-occurrence, particularly when the associations are used as an ecological indicator. Conversely, these results also indicate that mutual peaks in abundance can be missed under lesser sampling regimes. In this scenario, two species might appear to have greater niche differences than actually exist.

The effect of sampling scale on the relationship between AF and AS demonstrates that both can create the impression of significant co-occurrence between species. For instance, restricting sampling to the epilimnion created artificial coincident peaks in abundance in AF and AS during spring mixing. Indeed, Reynolds et al. (2002) classified AF and AS as a recurrent association because they both frequently occupy soft-water lakes during spring mixing. However, while few would restrict a sampling effort to late

mixing/early stratification, I restricted the data to that interval to show that the correlation of abundance between the two species across all lakes in both years was negative. This represents a relevant period in which the two species diverged in their ecology. In addition, the Jackson Lake analysis showed that high abundance of both species occurred after stratification, and independent of each other.

Analysis method

While presence/absence data can be a useful means to explore co-occurrence among species (Gotelli and McCabe, 2002), these results demonstrate that the infusion of a minimal amount of quantitative data into the frequency table analysis can change the perception of co-occurrence between two species. In particular, samples with high abundance of AF did not coincide with those of AS across the three lakes in both years. Correlation analysis also is commonly used to evaluate co-occurrence among species, however spurious correlations are common (Royama, 1992) and, in the assessment of synchrony, correlation can be high while other measures are low (Buonaccorsi et al., 2001). Indeed, correlation in the abundance between the two species was significant among many of the sampling regimes while the sign test was not. Mutual increase and decrease of abundance most closely matches the definition of synchrony (Buonaccorsi et al., 2001) and was more conservative than correlation in the assessment of species association in our analysis.

Clearly, as noted above, AF and AS have detectable differences in their distribution across the GYE lakes, undoubtedly facilitated by differences in their response to ecological gradients (Interlandi et al., 1999). This was most evident in the sign test analysis of synchrony, as the two species did not exhibit significant mutual changes in abundance over successive dates. However, changes in sampling intensity, and the use of presence/absence data and correlation analysis, produced the perception of co-occurrence between the two species.

Implications for sampling design

Many times, freshwater phytoplankton sampling efforts are constrained by resources, and investigators must optimize designs to collect information as efficiently as

possible. Here, I demonstrated that sampling intensity could influence the perception of a species distribution and therefore the perception of its ecology. While the probability of collecting species abundance maxima is greatest in the epilimnion, some species are more abundant in deeper waters (e.g. Gervais, 1998), including two dominant diatom species in the GYE lakes. Investigations of phytoplankton species distributions in lakes cannot ignore deeper waters, particularly when the euphotic zone extends to the metalimnion.

The number of species abundance maxima on each date was similar before and after stratification, emphasizing that some species are adapted to circulation (Chorus and Schlag, 1993). However, while abundance maxima were concentrated in the upper waters prior to stratification, the species distribution usually extended over the entire water column during mixing. This indicates that collecting samples at a single depth prior to stratification would be adequate in understanding population dynamics during mixing. On the contrary, reduction of temporal sampling intensity had a strong effect on detection of dominant species across the GYE lakes, particularly when the sampling interval exceeded 20 days. This sampling period is similar to the shortest duration of any of the dominant species in the water column.

The dataset of Interlandi et al. (1999) was uncommon in spatial and temporal frequency of sample effort and, for that reason, was used as a baseline in this study. Empirical data are available to speculate whether the intensity was adequate to capture all dominant species in the lake. Growth rates of phytoplankton species in culture range from 0.3 to 1.35 d^{-1} (Grover, 1989, Clegg et al., 2003, Gervais, 1997), but *in situ* are estimated to be no greater than 0.5 d^{-1} (Reynolds, 1993). At this rate, a species with a population size of one cell per liter would reach detection limit (one cell per 10 ml) within 12 days and potentially could reach dominance (10% of total biovolume, assuming average cell size and total biovolume) in another seven to nine days. Further, as noted above, the shortest duration of any of the dominant species was approximately three weeks in this study. It is probable, therefore, that the 7-day regime was fine enough to detect most, if not all, dominant species.

The phytoplankton communities of the GYE lakes are dominated by diatoms, likely a result of hydrological patterns (Interlandi et al., 1999), and flagellate dynamics were minimally explored in this study. Flagellates can control their position in a stable water column and can occupy a vertical plane as small as 1m (Gervais, 1998), indicating that the 5m sampling interval used in this study may not have been adequate to fully capture the distribution of flagellates.

Reduction of temporal sampling intensity increased the perception of coincident maxima. For instance, while most would consider a biweekly sampling schedule across seven depths to be an intensive effort, in this study it resulted in the false appearance of mutual abundance maxima for AF and AS during spring mixing. However, the overall number of joint maxima minimally increased under reduced sampling intensity across depth.

Coexistence is established through long-term stability of abundance or through recovery of members of the community that fall to low abundance (Chesson, 2000), and has never truly been explored in freshwater phytoplankton. While limited coexistence within a year (growing season) is possible, such as through the influence of a disturbance (Bowles, Chapter 3, this volume) or in cases of bluegreen bacteria dominance (Naselli-Flores, et al., 2003), it is inevitably temporary because it is destroyed by seasonal change. Rather, coexistence in variable systems, such as in the pelagia of lakes, is better approximated over long time scales (Chase and Leibold, 2003). Indeed, AF and AS have coexisted in Yellowstone Lake for over 350 years (Interlandi et al. 2003). The spatial and temporal separation of their abundance maxima within a year most certainly allows their coexistence in the lakes over time.

Coincident species maxima are likely the exception rather than the rule in communities structured by competition, so it is with little surprise that I find the identification of species co-occurrence could easily be a function of analysis method or inadequate sampling scale. The implication of these results also extends beyond phytoplankton to zooplankton (Havel and Pattinson, 2004) and fish (Sale, 1998) assemblages, and feasibly to any community that exhibits three-dimensional structure.

Because ecological investigations explore spatial and temporal patterns with no natural level of description (Hooper et al., 2005) and because each species experiences its environment at a unique scale (Levin, 1992; MacNally and Quinn, 1998; Wiens, 1989), the results of this study emphasize that species co-occurrence must be couched within a spatial, temporal, and statistical context.

Table 4.1. Julian date and depth of abundance maxima for *Asterionella formosa* (AF) and *Aulacoseira subarctica* (AS) under various sampling regimes across three lakes of the Greater Yellowstone Ecosystem. Coincident maxima are identified by matching symbols. All dates, all depths includes samples taken every 5 meters depth at one site on each lake approximately weekly (Yellowstone and Jackson) or every 10 days (Lewis) from ice-out to September or October. Multiple maxima are included when one or more abundance measurements were within 10% of the maximum measurement to allow for counting error. WCA = water column average.

Data subset	Yellowstone '96		Yellowstone '97		Jackson '96		Jackson '97		Lewis '96		Lewis '97	
	AF	AS	AF	AS	AF	AS	AF	AS	AF	AS	AF	AS
All dates, all depths	174, -5 174, -35	160, -15 160, -25 to -35	162, -20 to -50 212, -20	177, -40 177, -50	183, -5	211, -10 218, -10 254, -15	221, -5	148, -30	169, -5 176, 0 176, -10	187, -10 199, -20 211, -25	161, -5* 172, -10	161, -5*
Biweekly[1], all depths	174, -35	160, -15 to -35	212, -20	184, -45 to -50	159, -5 to -10	218, -10 254, -15	155, -5*	155, -5* 198, -5	-	-	-	-
Monthly, all depths	188, -50	160, -15 to -35	170, -25 to -30	199, -35 226, -20	173, 0	145, -5	169, 0	198, -5	199, -20*	199, -20*	182, -15	259, -20
All dates, 0m, -10m, -20m	167, 0 167, -10	160, -10	162, -20 212, -20	226, -20	159, -10 183, 0 183, -10	211, -10 218, -10	148, 0 169, 0 176, 0 176, -10	148, -20	176, 0 176, -10	187, -10 199, -20	172, -10	259, -20
All dates, surface	167	160	162	170	183	152	149 159 176	141 182	176*	176*	161 172*	172*
All dates, WCA	160*	160*	142*	142* 149 156 162	145*	145* 152	141* 148	141*	161*	161*	155*	155*

[1] Lewis does not change (10-day collections)

Table 4.2. Julian date and depth of abundance maxima for dominant species in Jackson Lake in 1997 under various sampling regimes. Coincident maxima in two or more species are identified by matching symbols. For instance, when all data are examined, coincident maxima appear between CB and *Eudorina* sp. on JD 256 at 5m depth. However, if the data are reduced as though sampling occurred at only three depths, the depth and date of the mutual maxima changes, and they converge with an abundance maxima of FC. Data include samples taken every 5 meters depth to 30 meters at one site on the lake weekly from 28 May to 13 September. Multiple maxima are included when one or more abundance measurements were within 10% of the maximum measurement to allow for counting error. Coccoid cyanobacteria and small flagellates were not included. SM = *Stephanodiscus minutulus*, AF = *Asterionella formosa*, AS = *Aulacoseira subarctica*, FC = *Fragilaria crotonensis*, CB = *Cyclotella bodanica*, WCA = water column average.

Data subset	SM	AF	AS	FC	CB	*Eudorina* sp.	*Dinobryon* sp.	*Anabaena* sp.	*Dactylo-coccopsis* sp.	*Aulaco-seira* sp.
All dates, all depths	141, -5	221, -25	148, -30	221, -10 246, -10	256, -5*	239, -5† 256, -5*	239, -5† 246, -5	239, 0	206, 0	234, -10
Biweekly[1], all depths	141, -5	155, -5*	155, -5* 198, -5	256, -15	256, -5†	239, -5‡ 256, -5†	239, -5‡	239, 0	214, 0	239, -10
Monthly, all depths	141, -5	169, 0	198, -5	256, -15	256, -5*	256, -5*	228, 0	198, 0	Not detected	228, -10
All dates, 0m, -10m, -20m	141, -10 141, -20	148, 0 169, 0 176, 0 176, -10	148, -20	221, -10 246, -10*	246, -10*	246, -10* 256, -10	246, 0	239, 0	206, 0	234, -10
All dates, surface	141*	148 169 176	141* 182	246†	239‡ 246†	256	246†	239‡	206	228 246†
All dates, WCA	141*	141* 148	141*	234‡ 256†	256†	256†	246	239	206	234‡

[1] Lewis does not change (10-day collections)

Table 4.3. Results of the frequency table analysis, Spearman rank correlation of abundance, and sign test analysis of mutual increase and decrease in abundance between *Asterionella formosa* and *Aulacoseira subarctica* under various sampling regimes. Data are from three lakes of the Greater Yellowstone Ecosystem from ice-out to mid-October in 1996 and 1997. JD = julian day, a = number of samples in which both species occur, p = total number of samples, Y = Yellowstone Lake, J = Jackson Lake, L = Lewis Lake.

GYE data used	Frequency table		Correlation		Sign test		
	Samples with both species present /total samples	sig. @ 0.01?	r_s	sig. @ 0.01?	# of "+"	# of "-"	sig @ 0.01?
All dates, all depths	659/690	Y	0.207	Y	314	326	N
All dates except Y97 JD142-170, all depths	-	-	0.087	N	-	-	-
JD 162-191, all depths	-	-	-0.244	Y	-	-	-
Before stratification[1], all depths	-	-	0.244	Y	-	-	-
After stratification, all depths	-	-	0.038	N	-	-	-
Bi-weekly[2], all depths	399/421	Y	0.233	Y	175	189	N
Monthly, all depths	199/216	Y	0.221	Y	94	83	N
All dates, 3 depths (0m, -10m, -20m)	241/259	Y	0.264	Y	112	124	N
All dates, surface	81/87	Y	0.257	Y	38	42	N
All dates, water column average	87/87	Y	0.128	N	39	40	N

[1] In Y96 stratification was in place on JD 188, in Y97 on JD 191, in J96 on JD 166, in J97 on JD 155, in L96 on JD 187 and in L97 on JD 182

[2] Lewis does not change (10-day sampling interval)

Figure 4.1. Correlation between *Aulacoseira subarctica* (AS) and *Asterionella formosa* (AF) abundance in three lakes of the Greater Yellowstone Ecosystem from ice-out to mid-October in 1996 and 1997. Samples were collected every five meters depth at one site on each lake. Y = Yellowstone Lake, J = Jackson Lake, L = Lewis Lake.

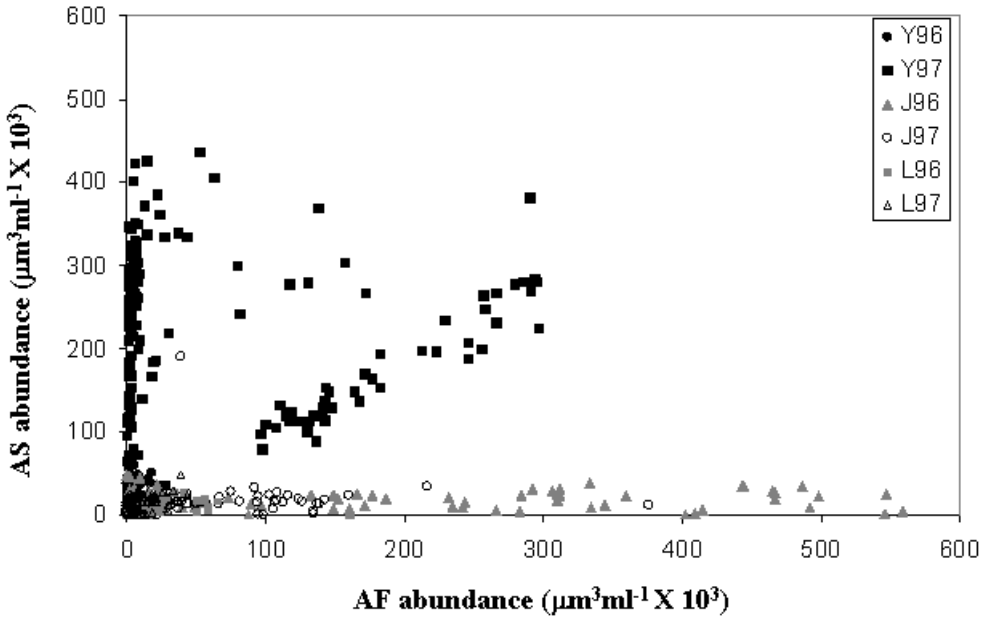


Figure 4.2. Date and depth of abundance maxima of the dominant species across Jackson Lake, Yellowstone Lake and Lewis Lake in 1996 and 1997. Multiple maxima for a species are shown if they were within 10% of the maximum to account for counting error, however if multiple maxima were contiguous by date or depth, only one is shown. The gray arrow represents the average date of stratification and the open arrow is the average depth of the upper boundary of the metalimnion.

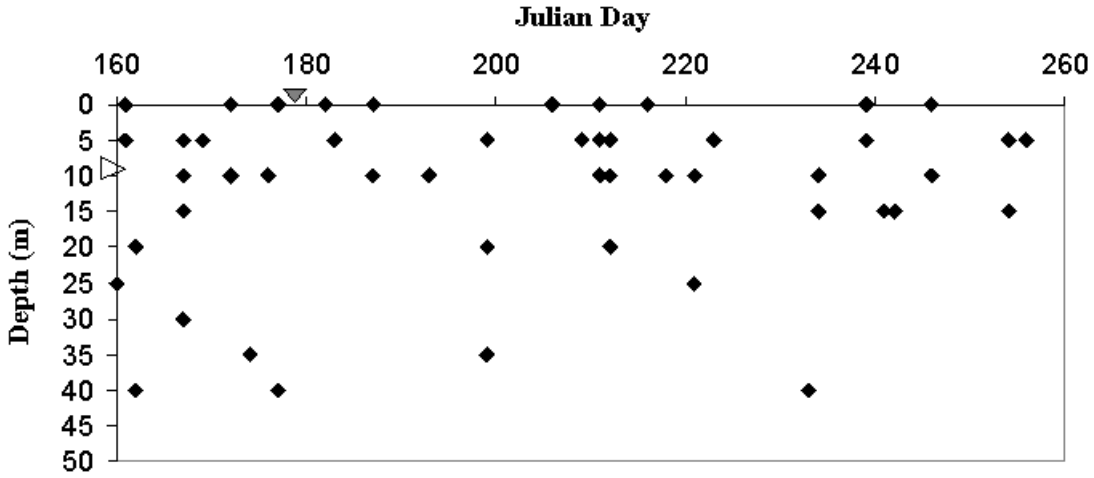


Figure 4.3. Number of dominant species identified during the lake year versus temporal sampling intensity across Jackson Lake, Yellowstone Lake and Lewis Lake in 1996 and 1997. A species was considered dominant if it comprised at least 10% of the total biovolume on any date (not including coccoid cyanobacteria).

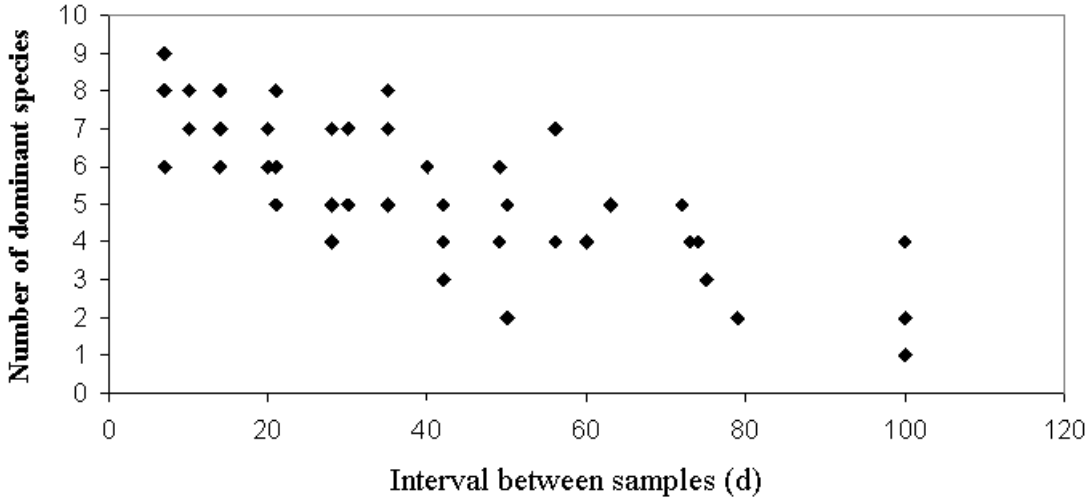


Figure 4.4. Frequency of joint abundance maxima versus temporal sampling intensity across Jackson Lake, Yellowstone Lake and Lewis Lake in 1996 and 1997. The frequency was calculated by dividing the number of joint maxima among the dominant species by the total number of pairings possible. The 100-d interval includes only one collection date in August.

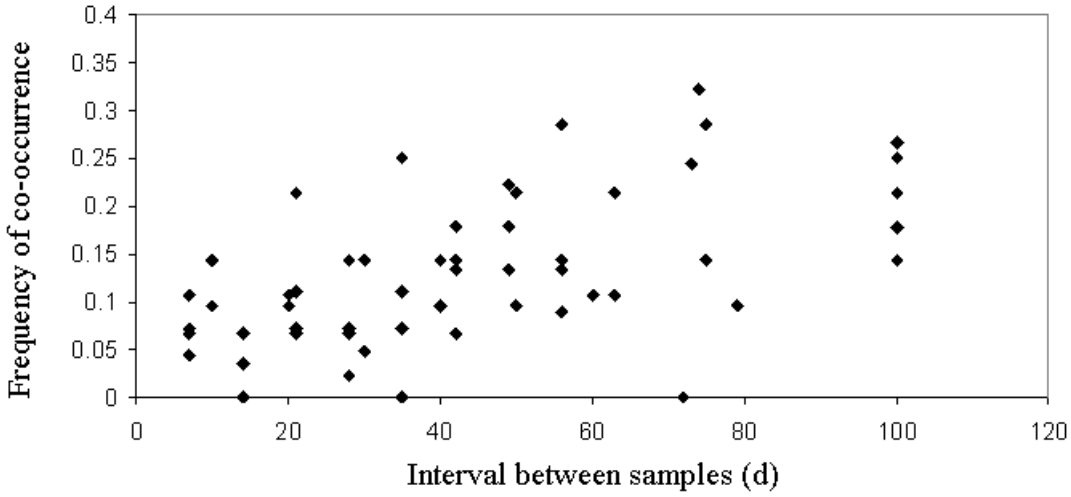
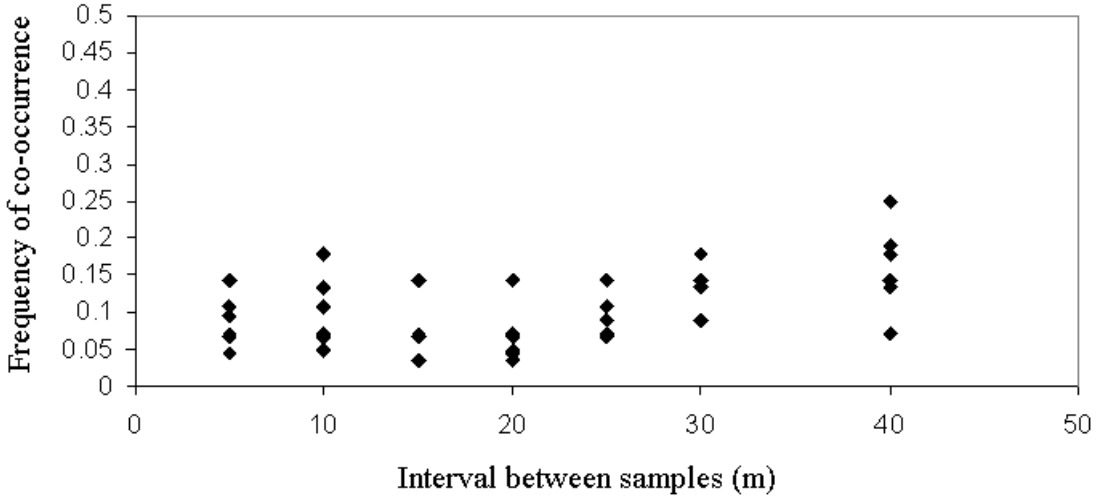


Figure 4.5. Frequency of joint abundance maxima versus sampling intensity across depth in Jackson Lake, Yellowstone Lake and Lewis Lake in 1996 and 1997. The frequency was calculated by dividing the number of joint maxima among the dominant species by the total number of pairings possible. The 40-m sampling interval includes only samples collected at the surface.



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